580

Vol. 19 No. 10

December, 1953

THE BOTANICAL REVIEW

Interpreting Botanical Progress

THE JOHN CREHAR LIBRARY
JAN 4 1954

The Cytogenetics of Triticale ..... JOSEPH G. O'MARA 587

Disease Resistance in the Vegetable Crops. II.
J. C. WALKER 606

FUTURE CONTENTS
ON INSIDE BACK COVER

Published Monthly except August and September at
111 E. Chestnut St., Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Founded in 1935 by
HENRY ALLAN GLEASON and EDMUND H. FULLING
Managed, edited and published at
The New York Botanical Garden
by
EDMUND H. FULLING

Advisory Editors

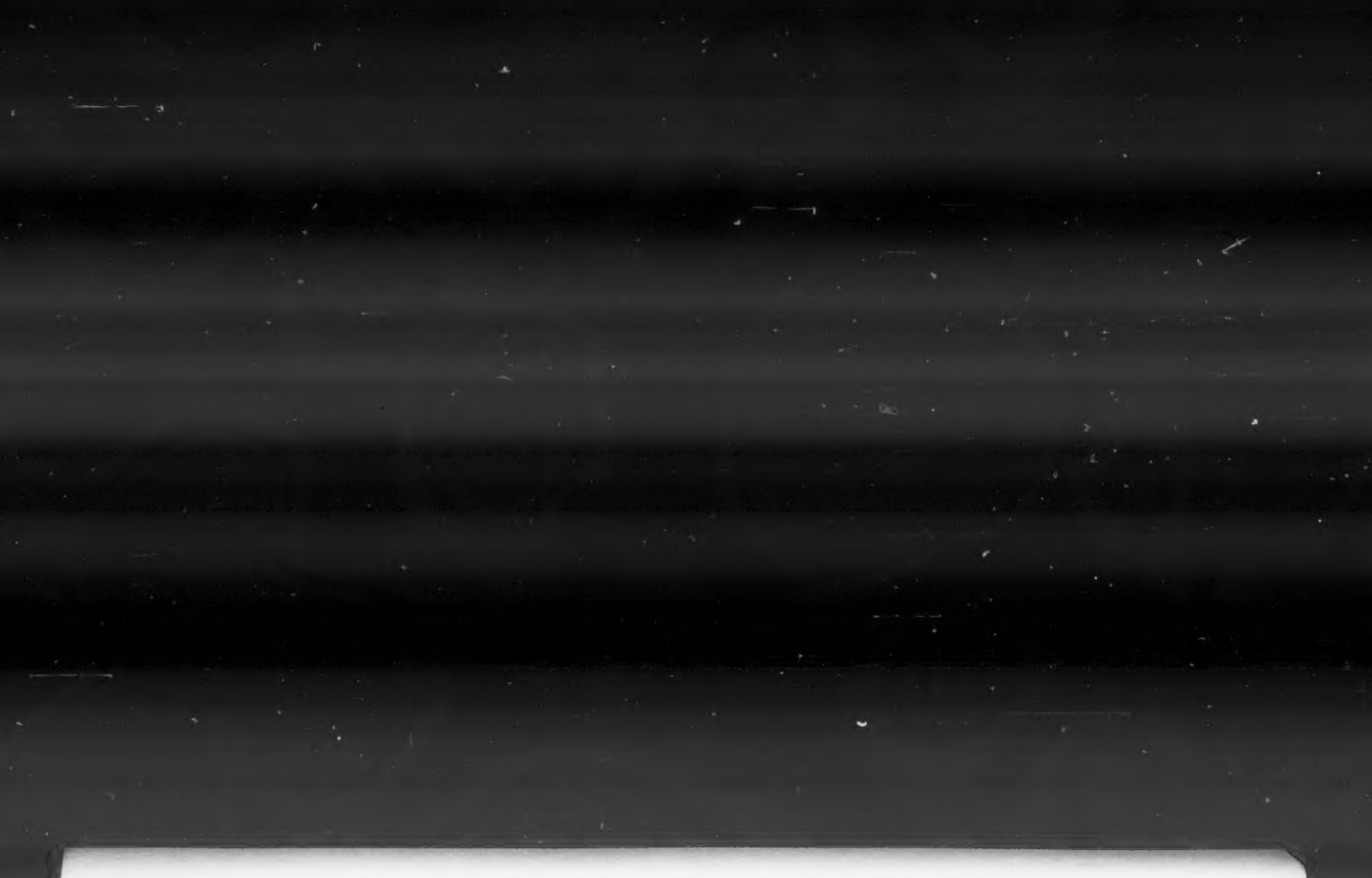
PROF. CHESTER A. ARNOLD
University of Michigan
PROF. MYRON P. BACKUS
University of Wisconsin
PROF. HERBERT C. HANSON
Catholic University of America
PROF. M. M. RHOADES
University of Illinois
PROF. GILBERT SMITH
Stanford University
DR. RUSSELL B. STEVENS
U. S. Government
PROF. S. F. TRELEASE
Columbia University
PROF. CONWAY ZIRKLE
University of Pennsylvania

THE BOTANICAL REVIEW is published monthly except August and September. Subscription rate for all countries is $6.00; single copies, 60¢. All subscriptions are payable in advance at par in Lancaster, Pa., or New York. Checks should be made payable to THE BOTANICAL REVIEW.

Articles are obtained primarily by invitation. Unsolicited manuscripts are also welcome. In all cases, however, the editor reserves the right to accept, reject or suggest revisions in submitted material. All manuscripts should be on double-space typewritten pages, with references and citations in accordance with the customary style of THE BOTANICAL REVIEW.

Missing numbers can not be supplied unless notice is received within two months after appearance of issues concerned.

All correspondence should be addressed to THE BOTANICAL REVIEW, at 111 E. Chestnut St., Lancaster, Pa., or Fordham P. O., New York, N. Y.



THE BOTANICAL REVIEW

VOL. XIX DECEMBER, 1953 No. 10

THE CYTOGENETICS OF TRITICALE *

JOSEPH G. O'MARA

INTRODUCTION

The hybrids between common wheat (*Triticum aestivum* L. emend. Fiori et Paoletti (= *T. vulgare*)) and common rye (*Secale cereale* L.) have been of both practical and theoretical interest. The agronomist has long been attempting to combine in one strain the quality and uniformity of wheat and the hardiness, vigor and disease-resistance of rye. The cytogeneticist has studied these two species in combination to ascertain the basic cytological phenomena of hybrids between species which are indisputably in different genera. The term Triticale, a compound of *Triticum* and *Secale,* was first used to designate the allopolyploid between *T. aestivum* and *S. cereale.* Since other allopolyploids between these genera are possible, the term must include all possible allopolyploids, and it will be used in this wider sense in this discussion. Since the behavior and properties of allopolyploids are related to the cytology of the undoubled hybrids, meiosis in the simple hybrids must also be considered in detail.

HISTORICAL

The historical aspects of this subject are of general interest because Triticale is probably the first "fixed" hybrid, *sensu* Burbank (1909), or allopolyploid, that was recognized as such. The first description of the simple hybrid is that of Wilson published in 1876. The hybrid was made after a series of observations on the structure of the flowers of wheat and rye and the changes that occur before anthesis and pollination (Wilson, 1874, 1875, 1876). The descriptions indicate that among the attempted crosses two indubitable successes occurred. These had the pubescent peduncle of rye and

* Journal Paper No. J-2189 of the Iowa Agricultural Experiment Station, Ames, Iowa. Project 1181.

came from seeds produced by wheat plants. The description accords well with the experience of all later investigators. The first illustration of the hybrid is that of Carman in 1884. The illustrations show that, although most of the attempted crosses were actually contaminations, one true hybrid was obtained. The evidence of hybridity is the low fertility of but 1.9 seeds per head and the characteristic rye pubescence on the peduncle in plants from wheat as the female parent. The amphidiploid, or allopolyploid, was first discovered by Rimpau in 1888, and described in 1891. The published report indicates that Rimpau discovered not an amphidiploid individual but a doubled sector on a simple hybrid plant. From 15 seeds he secured three plants which were undoubted back-cross contaminations to wheat, and 12 which were very uniform in appearance and very much like the hybrid from which they came. These 12 amphidiploids are probably the first observed in culture, i.e., the first new species to be observed in origin. The Rimpau Triticale illustrated well the constancy found in all later allopolyploids, having been propagated by seed to the present day with no detected deviation from its original behavior or variation in its original structure intermediate between wheat and rye. Many other Triticales have been produced since by cereal agronomists and cytologists (Müntzing, 1939).

The hybrid between *T. durum* Desf. and *S. cereale* L. was reported by Aase in 1930, and the derived allopolyploid by O'Mara in 1948. The hybrid between *T. monococcum* L. and *S. cereale* L. has not been reported. The hybrid between *T. Timopheevi* Zhukov. and *S. cereale* has been described by Kostoff (1937). Therefore, of the four genomes recognized within the genus *Triticum, S. cereale* has been combined with the ABD genomes of *T. aestivum,* the AB genomes of *T. durum,* the AG genomes of *T. Timopheevi,* but not with the A genome of *T. monococcum.*

THE TRITICALE COMPONENTS

TRITICUM AESTIVUM L. Cultivated bread wheat was designated *Triticum aestivum* by Linnaeus but was later named *Triticum vulgare* by Villars. Among American agronomists the later name, *T. vulgare,* is in such common use that it has displaced *T. aestivum* in almost all agronomic writing in the United States. European investigators, however, customarily refer to cultivated bread wheat as *T. aestivum,* the proper official name according to the interpretation

of Schiemann (1952) of the International Rules of Botanical Nomenclature. *Triticum aestivum* and *Triticum vulgare* are, therefore, synonyms, and the hybrids with rye are identical from either taxonomic or agronomic viewpoints.

The chromosome number of *T. aestivum* is 42 or 21 pairs. These 21 pairs have been shown to consist of three distinct genomes of seven chromosomes each (Sax, 1922; Kihara, 1924; Lilienfeld and Kihara, 1934.) The genomes were designated A, B and C by Gaines and Aase (1926), and A, B and D by Kihara (1924). The custom among American and British cytologists has been to use the A, B, C designations, but the A, B, D notation has priority, and C is more properly used for the seven-chromosome genome of *Aegilops caudata* L. The designations of the seven-chromosome genomes in the Triticinae has been critically discussed by Sears (1948). The genome designated A is found in the seven-chromosome species of which *T. monococcum* is a typical representative (Sax, 1922; Kihara, 1924). The genome designated B is now unknown or has been so altered as to be undetectable by the usual methods (McFadden and Sears, 1946). Genomes A and B together constitute the 14-chromosome species, of which *T. dicoccoides* is a typical representative. The D genome constitutes *Aegilops squarrosa* L. (Kihara, 1944; McFadden and Sears, 1944, 1946). These relationships were discovered independently in studies of hybrids and by the synthesis by McFadden and Sears of *Triticum spelta* L., a species homologous with *T. aestivum* L. and which may be considered identical with it in phylogenetic studies.

TRITICUM DURUM DESF. This species has 28 chromosomes, or 14 pairs. These pairs were shown to consist of two different seven-chromosome genomes (Sakamura, 1918; Sax, 1922; Kihara, 1924) which are now designated A and B and are homologous with two of the three genomes in *T. aestivum* L.

SECALE CEREALE L. This species, common rye, has 14 chromosomes or seven pairs. The genome at present has no known homologous genome among the investigated cereals and cereal relatives (Kihara, 1924; Zalensky and Doroshenko, 1925; Meister and Meister, 1924; Thompson, 1926, 1931; Bleier, 1930, 1933; Melburn, 1929; Aase, 1930; Longley and Sando, 1930; Plotnikowa, 1931; Florell, 1931; Lebedeff, 1932, 1933*a*, 1933*b*; Kattermann, 1934*a*, 1934*b*; Kagawa and Chizaki, 1934; Liljefors, 1936). The

few pairs reported by some of these investigators are now not thought to be due to inter-generic homology but to some form of intragenomic homology made evident because the hybrid microsporocyte allowed no normal homologous association to occur and thus permitted remote homologies to be realized (Thompson, 1931). This type of pairing has been termed homoeologous (Huskins, 1946), homoeologous chromosomes being those which once were homologous, i.e., essentially identical, but have become so different that they rarely pair.

CYTOLOGY OF THE HYBRIDS

The hybrids which when doubled constitute the known Triticale combinations exist with both the tetraploid (*T. durum*) and the hexoploid (*T. aestivum*) varieties. The combination of *T. durum* and *S. cereale* has been made much less frequently than that involving *T. aestivum*, owing to hybridization difficulties. It has been made by Aase (1930), Plotnikowa (1930), Kagawa and Chizaki (1934) and O'Mara (1948). The undoubled hybrid itself, according to these investigators, may show several pairs at meiosis, but there would seem to be nothing in the frequency of pairs which could not be explained by autosyndesis within species genomes. The hybrid has also been made with other wheats with the same genome constitution (AB). Such hybrids involve *T. dicoccoides* Körn (with *S. montanum*) (Longley and Sando, 1930), *T. polonicum* L. (Plotnikowa, 1930) and *T. turgidum* (Liljefors 1936). The tetraploid wheat species *T. Timopheevi* Zhuk. which has the genomic formula AG has also been hybridized with *S. cereale*. The pairing also indicates no *Triticum-Secale* chromosome homology (Kostoff, 1937).

The hybrids involving the hexaploid wheats have been made much more frequently than those with the tetraploid wheats, presumably because the hexaploids are more important from the viewpoint of agronomy. The combination with *T. spelta* L. has been made by Aase (1930) and Kagawa and Chizaki (1934). Both investigations showed that most meioses had no pairs and that the highest pair number was four. Such pairs as did occur were probably between homoeologous chromosomes within genomes or between intra-specific genomes. The hybrid with *T. compactum* Host., another hexaploid, was studied by Florell (1931), Kagawa

(1933) and Kagawa and Chizaki (1934), all of whom found that meiosis was similar to that described in the *T. spelta* hybrid. Most of the combinations have been between rye and *T. aestivum,* this combination being made many times, owing to the importance of bread wheat in all parts of the world. The cytological examinations of the hybrids have been made to determine homologies and to ascertain whether crossing over and gene exchange could be expected in the hybrid. Such gene exchange would permit the introduction of rye genes into wheat, an event which would be of great agronomic importance if possible. The cytological observations all indicate that the number of chromosome pairs is so low that homoeologous intra-specific pairing can account for all that are seen (Kihara, 1924; Zalensky and Doroshenko, 1925; Meister and Meister, 1924; Thompson, 1926; Melburn, 1929; Bleier, 1930, 1933; Aase, 1930; Longley and Sando, 1930; Florell, 1931; Lebedeff, 1932, 1933, 1933; Kattermann, 1934, 1934). The hybrid with *S. montanum* indicates that it is identical with *S. cereale* at meiosis in hybrids with *T. aestivum.* The explanation of autosyndetic pairing was presented by Thompson (1926) and, though it contradicts the interpretations of some earlier investigations, is now generally accepted by cereal cytologists (Sears, 1948).

The evidence for the interpretation of the chromosome pairs found in the various *Triticum-Secale* hybrids comes from the character of meiosis in cereal haploids. Although the regular pairing in diploids would seem to indicate that effective homology within a genome could not exist, adequate observations show that intra-genomic associations do occur when normal pairing is not possible. In species hybrids and in haploids each chromosome has no homologue and consequently may realize weak and obscure homologies which would be wholly ineffective in normal meiosis when each chromosome has a homologous partner with which its normal affinity is satisfied. While the theory of autosyndetic association is plausible (Thompson, 1926), the possibility also exists that some seemingly homologous association between non-homologous chromosomes may actually be an expression of a tendency to random and irrelevant pairing which manifests itself when a true homology can not be realized. That such pairing is probably non-homologous instead of homoeologous is indicated by intra-chromosomal pairing in *Zea mays.* In monosomic plants the chromosome

without a homologue is found folded back on itself. The association is not constant in configuration, as homeology would produce, but is of various kinds which indicate that almost any part will pair with another within the possibilities of the structure (McClintock, 1933). Whatever the nature of the pairing, homoeologous or non-homologous, so little of it occurs in the hybrid that it can be accounted for wholly by pairing within genomes instead of between genomes. In cereals such intragenomic pairing has been reported in *Hordeum distichum* (Tometorp, 1939), *Hordeum vulgare* (Inouye, 1933), in *Triticum monococcum* (Katayama, 1935; Smith, 1946), in *Triticum durum* (Kihara, 1936), in *Triticum aestivum* (= *vulgare*) (Gaines and Aase, 1926; Kostoff, 1939; Krishnaswamy, 1939; Raw, 1937; Yamasaki, 1936); in *Secale cereale* (Nordenskiöld, 1939; Levan, 1942).

In *T. aestivum* the maximum number of pairs reported in a haploid was nine by Krishnaswamy. This represents an extreme which may have an explanation in some unusual characteristics of the material. Most observers indicate that four or five pairs is probably the maximum for any wheat-rye hybrid. In *S. cereale* the usual maximum is two bivalents in the haploid, but as many as three associations have been reported (Levan, 1942). A trivalent association also occurs infrequently in haploid *T. aestivum* (O'Mara, unpublished). That these associations are the result of chromosome pairing and chromatid exchange is indicated by the occurrence in the progeny of haploids of reciprocal translocation which are most easily accounted for by crossing over between non-homologous chromosomes (Sears, 1939). In the simple hybrid, therefore, the total number of chromosome associations can be arrived at without assuming any hybrid associations. The maximum reported by various investigators of the hybrid are three or four, numbers which are not more than the total of the associations characteristic of the two species as haploids.

GENETICS OF THE HYBRIDS

The genes of rye would be very valuable in wheat which is deficient in many characters that are expressed to an extreme degree in winter rye. Such characters are winter hardiness, insect resistance or tolerance, disease resistance and the ability to thrive on poor soils. Agronomists, therefore, have been interested in

transferring to wheat the genes which give rye these desirable characteristics. The true results of the investigations are difficult to evaluate. Many of the experiments were performed at times when the basic cytological phenomena of hybrids were unknown, and consequently what precaution was taken to ensure correctness of interpretation was not recorded and now is not known. The result has been that wheat improved by rye has been recorded in several instances, but the possibility is not excluded that the different variety extracted could have been improved by an unrecognized and unrecorded pollination of the hybrid by another wheat strain. The first of these was that reported in 1884 by Carman, and it may typify many of those that followed. The hybrid was made by artificial pollination and was self-sterile in that the anthers shed no pollen. Such male sterile plants, however, are not wholly female sterile. They will set a few seeds when pollinated artificially or under field conditions when wheat pollen is abundant enough so that most flowers receive some pollen. When the pollen source is uncontrolled, as in open pollination under field conditions, what may be produced is essentially a wheat hybrid, one parent of which is unknown, plus from zero to seven univalent rye chromosomes. How much the characteristics of the hybrid are to be attributed to the rye chromosomes and how much to wheat hybridity can not be easily known. The florets of the sterile hybrid remain open with receptive stigmas for many days, and wheat pollen from diverse distant sources may finally reach the florets. A different segregate in later generations could be the result of many different processes. It could be the result of simple recombination, of intra-chromosomal duplications or deficiencies, of the production of isochromosomes with the corresponding loss of whole chromosome arms, or of insertion of rye genes into wheat. That such rye insertion does not frequently occur, if it occurs at all, is indicated by the fact that no known wheat variety in the New World is known to have been improved by rye in spite of many extensive attempts to put rye genes into wheat. Thus the original variety Twentieth Century, which was known under several names, although descended from a wheat-rye hybrid, had no superiority indisputably of rye origin. The extensive nature of the attempts made is obscured by the failure of investigators to report lack of success, but innumerable attempts have been made by agronomists to obtain in wheat re-

sistance to Hessian fly, winter hardiness, ability to grow at low temperatures, rust resistance and ability to grow on land of low fertility, among other desirable rye characteristics. The uniform failure of these attempts must mean that gene transfer is extremely rare or impossible for these characteristics. Whether other characteristics determined by fewer genes or one gene could be transferred at meiosis remains to be studied. The data all indicate that the probability of success, without recourse to artificial means, like radiation, is very small. Among the attempts, the following have been recorded—Carman, 1884; Guard, 1938; Meige, 1937; Derzhavin, 1938; Meister, 1936. Strains which possess the rye gene or genes responsible for the pubescent peduncle have often been transferred to wheat. These genes, however, have not been incorporated in the wheat genome but have been added to wheat in whole rye chromosomes or chromosome arms. These additions, therefore, do not represent exchanges of genes between wheat and rye, and do not indicate homology. Addition of this rye character to wheat has been recorded by many investigators (Love and Craig, 1919; Leighty and Taylor, 1924; Florell, 1931*a*, 1931*b*; Tschermak, 1931; Taylor, 1934; Kattermann, 1934*a*; Oehler, 1931*a*, 1931*b*, 1934*b*, 1935, 1937*a*, 1937*b*, 1938; Ledingham and Thompson, 1938). Successful transfer of rye genes to wheat or wheat-like derivatives from the hybrid has been recorded by Russian investigators (Meister, 1921; Meister and Meister, 1924; Meister, 1926; Meister and Tjumjakoff, 1927, 1928). The recent Russian strains have not been available for study, so little is known of their cytological characteristics. The lines described by Meister were studied by Bleier (1933) who concluded that no rye genes had been incorporated in these improved lines. Bleier concluded that the improved lines derived their superiority not from rye but from recombinations between genes of the wheat in the hybrid with rye and genes of another wheat which had pollinated the hybrid. The lines were also studied by Vakar and Krot (1934) who found meiotic anomalies in the strains. The authors concluded that interchanges between wheat and rye chromosomes had occurred. That such interchange could be possible would seem to be indicated by the occurrence of non-homologous pairing in maize (McClintock, 1933) and by the occurrence of reciprocal translocations between wheat chromosomes in the progenies of wheat haploids (Sears, 1939). The intrageneric

translocation might be produced by natural radiation. Since it has not occurred in many investigations the probability of success could be very low, so low as to be quite impractical. The possibility of producing such intercalations of rye into wheat by artificial means seems to be of usable magnitude. The hybrid has one-fourth rye chromosomes, and if chromosome breaks are at random, the rye chromosome segments should be attached to wheat relatively frequently. That such changes are possible is shown by the viability of whole chromosome deficiencies in wheat (Sears, 1939, 1944) and of rye additions, vide supra.

CYTOLOGY OF TRITICALE

The cytological details of meiosis in Triticale are of interest because the fertility of the allopolyploid combination depends on a normal meiotic division. Since Triticales are not fully fertile, the nature of the anomalies is important if remedial plans or manipulations are to be designed. The simplest and least informative of the studies consists of determining the chromosome numbers of populations from Triticales which have been through one or more sexual generations. Such data indicate the amount of numerical chromosome constancy in the material but must always underestimate the true amount of anomaly. The chromosome number in Triticale should be 56, which is twice the total gametic sum of the parents. If the meiosis were wholly normal, the cells at meiosis would have 28 pairs and each gamete would contain 28 different chromosomes, of which 21 would be wheat and seven would be rye. This allopolyploid, however, is not perfect and univalents do occur at meiosis. The number is different for different Triticales, but all have some. Thus the Wiebe strain, which was examined by Müntzing (1939), had an average of 1.88 univalents per meiosis, and the Rimpau strain showed 6.10 univalents per meiosis. The maximum value extended as far as 18 univalents for the Wiebe strain and 12 for the Rimpau strain. The gametes from such meioses frequently have, therefore, anomalous chromosome numbers. Most of the male gametes that function are euploid or nearly so, owing to the strong selection in favor of euploid pollen, but the female gametes can function with much anomaly and are not subject to competition. The result, therefore, is that numbers other than 56 are frequently found (Berg and Oehler, 1938). Since

euploid gametes are more successful in competition in the cereals, the aneuploid plants are probably less fertile than the euploid ones, and some constancy in chromosome number is maintained. However, the failure to secure precise euploid numbers for the gametes is not the only source of cytological anomaly in this allopolyploid. The occurrence of univalents has been recorded by many observers (Lindschau and Oehler, 1935; Müntzing, 1939). As has been shown in various species, univalent chromosomes can be a source of anomaly other than that which is simply numerical. The most simple example of such anomaly is the duplication and deficiency of different chromosomes so that the total number is unaltered. Such changes have their parallel in the nullisomic-tetrasomic combinations in *Triticum aestivum* (Sears, 1944). If such alteration is possible in a pure species which should be sensitive to deficiency and duplication even though polyploid, it should be less noticeable in its effects than such alteration in a new allopolyploid which consists of two independent and unintegrated genomes. That such duplication and deficiency may occur is shown by the occurrence of quadrivalents and trivalents in Triticales A and C, the Rimpau and Wiebe strains (Müntzing, 1939). Another kind of duplication and deficiency which occurs as a result of meioses with univalent chromosomes is caused by irregular divisions of the univalents so that isochromosomes are formed. Such division of univalents has been reported in many species (Upcott, 1937; Darlington, 1940; Sears, 1944; O'Mara, 1951). The consequence of such misdivision is that the kind of deficiency and duplication is more difficult to detect because the characteristic quadrivalents of whole chromosome duplication and deficiency do not occur. What is now present in the quadruple condition is one chromosome arm, and such a constitution can lead only to bivalent formation. The deficiency, consequently, would be for but two homologous chromosome arms. These changes are all concealed under normal chromosome numbers and would not be discovered readily because the allopolyploid is not regular meiotically, and these derived anomalies would have to be distinguished from the irregularities usually present at meiosis, i.e., those which occur at the first meiosis after chromosome doubling before any misdivision products or other anomalous chromosomes could occur in the meiotic cells. Although pollen selection in favor of normal pollen and the higher fertility of individuals with complete chromosome complements will generally result in

populations which are uniform in appearance, the probability can not be negligible that the gametes and zygotes can tolerate misdivision products. This conclusion seems to be indicated by the fact that *Triticum aestivum* will tolerate without serious results half-chromosome deficiencies, and in some instances plants can be secured which are deficient for two whole chromosomes. An allopolyploid, therefore, should be able to endure at least as much deficiency as the constituent species, and what deficiency does occur should be difficult to observe phenotypically because the organism has two full genomes which must, to some extent, mask each other's deficiencies. The apparent uniformity of the Triticale amphidiploid can not indicate absolute uniformity in the chromosome constitution, for the production of viable and functioning aneuploid gametes has been demonstrated (Müntzing, 1939).

The *Triticum durum–Secale cereale* combination has not been studied cytologically at the allopolyploid level. It seems to be similar to the *T. aestivum–S. cereale* combination in uniformity and in partial sterility, but careful observations have not been made. It is no more fertile than the original Triticale combination (O'Mara, 1948).

ORIGIN OF TRITICALE

Since the genetic nature of allopolyploids is related to their mode of origin, the methods used or the events which occurred in producing the various Triticales is of interest. The first Triticale known, the Rimpau strain, was reported by Rimpau to have been found in seed from an F_1 plant. Among 15 seeds secured, three were undoubtedly back crosses to wheat, but twelve resembled the F_1 very much and were "untereinander sehr ahnlich". This mode of origin, that of somatic doubling in the hybrid with its concomitant male and female fertility, is the common method (Rimpau, 1891; Dorsey, 1936; Müntzing, 1936). Its genetic consequences are the most easily predictable, the progeny of the plant being homozygous in the absolute sense, since each locus is represented by two genes which descended from the same gene in the immediately preceding generation. With these individuals the homozygosity must be free from undetectable gene constitutions which simulate homozygosity, isoalleles and other kinds of genes demonstrable only under conditions unusually favorable for experimentation. Unfortunately, however, the somatic doubling itself produces

meiosis with the full chromosome complements of the allopolyploid in which the pairing is not regular nor are the disjunctions normal. The consequence is that, although the homozygosity is theoretically absolute, it may be quite confounded with various comparatively gross cytological anomalies. Obviously, even though somatic doubling would seem to ensure homozygosity, the Triticale strains can not be considered as uniform in genetic constitution after one meiosis has occurred.

Another possible method of origin is that used by Müntzing (1939) who crossed Triticale with *Triticum aestivum* and recovered 56-chromosome individuals in F_2 populations. The method as described requires a Triticale strain as a parent of a new strain. The same result should be attainable by crossing the undoubled F_1 hybrid with *T. aestivum*. The F_1 hybrid produces unreduced eggs which are similar to the eggs produced by Triticale, and the combination of such eggs with *T. aestivum* should produce hybrids like those involving Triticale and *Triticum*.

The method used in other genera, of crossing two autotetraploids to produce an allopolyploid, has not been used to produce Triticale because tetraploid *T. aestivum* does not produce viable gametes (Dorsey, 1936).

Other methods of producing constant wheat-rye hybrids may be discovered, but the simple one of doubling the chromosome complement of the F_1 hybrid with colchicine would seem to be direct and dependable enough for most purposes. The most difficult report to reconcile with the known reports on this subject is that of Lewitsky and Benetzkaja (1931) who report a uniform Triticale population from an F_1 which was male sterile. Such sterility would seem to exclude the union of unreduced gametes or of gametes produced from tissues with doubled chromosome complements.

GENETIC CHARACTERISTICS OF TRITICALE

The term " genetic " here is used in a broad sense to indicate the behavior in hybrid combinations. The numbers of usable genes in rye and wheat at present is too low to permit extensive exact genetic experiments with Triticale. The available data are to be found in the work of Müntzing (1936, 1939).

The fertility of the strains is of interest from a practical viewpoint because a minimum fertility must exist if the strain is ever to be used directly for grain. The variation in pollen fertility

ranged from 70 to 92.5 per cent. This estimate must be one of maximum fertility because many normal appearing grains never germinate or germinate so slowly that they may be considered to be non-functional, since they would not reach the egg even without competition. The hybrid Triticales, which included eight combinations, were all at least as pollen-sterile as the parental strains.

In seed setting, which may indicate the amount of female fertility, the parental strains had about one and one half seeds per spikelet. The F_1 combinations had an average of one seed per spikelet. The hybrid Triticales, therefore, are more sterile than the parental strains. This unpredictable sterility would seem to show that the homozygosis of the parental strains is not the cause of the sterility. Later examination of other allopolyploids in which both component species are normally self-pollinated and therefore homozygous demonstrated that partial asynapsis or desynapsis is characteristic of almost all allopolyploids (Sears, 1941).

The Triticale allopolyploid is unusual in that one of its components, *S. cereale,* is normally self-sterile and therefore very heterozygous. The implication of such a genetic constitution is that deleterious genes are common in the population but masked by normal dominant alleles. The consequence should be that the Triticale constitution should be one which is homozygous for such deleterious genes and that some of these could affect meiosis directly or indirectly. A test of this hypothesis is available in crosses of unrelated Triticale strains. The tests showed that the hybrid Triticales have more meiotic irregularity than the original homozygous strains—so the hypothesis must be rejected and the meiotic irregularity ascribed to some other phenomenon.

The vigor of the F_1 Triticale hybrids is greater than that of either parent, a result which seems reasonable when the facts are considered that each Triticale consists of a homozygous wheat complement plus a homozygous rye complement, and that each of these complements is associated with heterotic effects in the pure species when heterozygous.

PARTIAL TRITICALE COMBINATIONS

By partial Triticale is meant those types in which one component or both are not present in the full normal complement. Among these would be included kinds which have been designated alien addition strains and alien substitution strains in *Nicotiana* by R. E.

Clausen (Gerstel, 1945). The alien addition strains, involving addition of rye chromosomes to wheat, undoubtedly were observed many times before their cytological basis was understood. Unfortunately rye chromosomes individually do not seem to have marked phenotypic effects. The consequence is that, with one exception, the addition races are very much like normal wheat. The exception is the race which carries chromosome I of rye. This chromosome has in its long arm a gene, or gene complex, which produces pubescence on the peduncle (O'Mara, 1951). The effect is unmistakable and the presence of the rye chromosome arm can invariably be determined by its phenotypic effect. This pubescence was found in the derivative strains of wheat-rye hybrids before the chromosomal basis was understood, and was naturally considered to be a transfer of rye genes into wheat (Gaines and Stevenson, 1922; Leighty and Taylor, 1924; Taylor, 1934; Kattermann, 1935). The transfer was considered interesting chiefly because it demonstrated gene interchange between the two genera to be possible. Later investigations showed that interchange had not occurred but that blocks of rye genes had been added to the wheat genome. These blocks were whole rye chromosomes or chromosome arms (Florell, 1931; Kattermann, 1934, 1935, 1937*a*, 1937*b*; Ledingham and Thompson, 1938; O'Mara, 1940, 1951). The phenotypic character pubescent peduncle, hairy neck or "Behaarung des Halmes" is produced by one rye chromosome. The rye chromosome containing the gene consists of two very unequal arms, but a conspicuous secondary constriction makes the chromosome seem isobrachial. The gene for pubescence was found in the long arm (O'Mara, 1951). In addition to the pubescence, the rye chromosome produces other alterations in wheat. These effects are mostly assignable to a shortening or compressing of the internodes. The effects were also ascribable to the long arm of chromosome I. The short arm seemed to have little or no detectable effect in one or two doses. The long arm when present twice had all the obvious effects of two whole chromosomes. The possible kinds of addition of this one rye chromosome, of its component arms as telocentric chromosomes, and of the derivatives as isochromosomes, have been illustrated (O'Mara, 1951). The number of kinds of addition for one chromosome is five, if the additions be limited to the hemizygous condition, or ten if each addition be allowed a homologue. If all

seven rye chromosomes be considered, the number of hemizygous additions becomes 35. Some of these will probably be unstable, like the univalent derivatives in wheat (Sears, 1952). Since the rye chromosome often occurs in the univalent condition, even when it is present as two homologues, stable additions of the chromosome to wheat would seem to be improbable.

The alien substitution races involve the same rye chromosome, presumably because it contains the only known marker gene or genes which are readily detected phenotypically. The substitution races contain 21 pairs of chromosomes, 20 wheat pairs and one rye pair. They have been derived in two ways—from wheat-rye hybrids and addition races (Kattermann, 1938) and from backcrosses of Triticale to *Triticum* (O'Mara, 1946).

The characteristics of the substitution races seem to be unpredictable from the effects of addition. Two addition doses produce sterility and semi-dwarfness, but two substitution doses produce little or no sterility and no dwarfness. The number of possible substitutions is much greater than that of additions. If only whole chromosome substitutions be considered there are 147 possible homologue substitutions—seven rye chromosomes for each of the 21 wheat chromosomes. At present only one known substitution has been determined, that of chromosome I of rye for chromosome IX of wheat. Since the 21 monosomic stocks of wheat have been extracted and identified (Sears, 1952), all the substitutions of chromosome I of rye for each of the 21 wheat chromosomes should be possible. A hybrid of the substitution race involving chromosome IX of wheat crossed to a wheat gamete nullisomic for any wheat chromosome other than chromosome IX will produce at meiosis 19 bivalents plus univalents representing chromosome I of rye, chromosome IX of wheat, and the wheat chromosome to be eliminated. Among the progeny obtained by selfing this plant will occur individuals which have regained both homologues of chromosome IX, both homologues of chromosome I of rye, and no member of the pair missing in the monosomic or nullisomic stock (O'Mara, unpublished).

The Triticale allopolyploid in its various forms is perhaps capable of more cytological manipulation than any other at present available.

BIBLIOGRAPHY

1. Aase, Hannah C. Cytology of hybrids. Res. Stud. Sta. Col. Wash. **2:** 1–60. 1930.
2. Berg, K. H. v., and E. Oehler. Untersuchungen über die Cytogenetik amphidiploider Weizen-Roggen-Bastarde. Züchter **10:** 226–238. 1938.
3. Bleier, H. Untersuchungen über das Verhalten der verschiedenen Kernkomponenten bei der Reduktionsteilung von Bastarden. Cellule **40:** 82–144. 1930.
4. ———. Genetische und zytologische Untersuchungen von Weizenstämmen aus Weizen-Roggen Bastardierungen. Zeits. Zücht. A. **18:** 191–211. 1933.
5. Burbank, L. Am. Breeders' Assoc., Rep. **5:** 40–43. 1909.
6. Carman, E. S. Rural New Yorker 420, 452, 484, 557, 656, 688. 1884.
7. ———. Ruralisms. Rural New Yorker **53:** 634–635. 1894.
8. Darlington, C. D. The origin of isochromosomes. Jour. Genet. **39:** 351–361. 1940.
9. Derzhavin, A. Results of work on breedig perennial varieties of wheat and rye. Bull. Acad. Sci. **1938:** 663–665. 1938.
10. Dorsey, E. Induced polyploidy in wheat and rye. Jour. Hered. **27:** 155–160. 1936.
11. Florell, V. H. A genetic study of wheat-rye hybrids and back crosses. Jour. Agr. Res. **42:** 315–339. 1931,
12. ———. A cytologic study of wheat-rye hybrids and back crosses. Jour. Agr. Res. **42:** 341–362. 1931.
13. Gaines, E. F., and Hannah C. Aase. A haploid wheat plant. Am. Jour. Bot. **13:** 373–385. 1926.
14. ——— and F. J. Stevenson. Rye-wheat and wheat-rye hybrids. Jour. Hered. **13:** 81–90. 1922.
15. Gerstel, D. U. Inheritance in *Nicotiana Tabacum*. XX. The addition of *Nicotiana glutinosa* chromosomes to tobacco. Jour. Hered. **36:** 197–206. 1945.
16. Guard, A. T. Studies on cytology and resistance to leaf rust of some interspecific and intergeneric hybrids of wheat. Am. Jour. Bot. **25:** 478–480. 1938.
17. Hoover, M. M. Wheat-rye hybrids. Jour. Hered. **20:** 171. 1929.
18. Inouye, C. Meiotic mitosis in *Hordeum sativum*. Miyazoki Coll. Agr. & For. Bull. **5:** 77–96. 1933.
19. Kagawa, F. Zytologische Studien über Ausbildung der Pollenkörner bei *Triticum compactum* × *Secale cereale*. Proc. Soc. Crop Sci. Japan **8:** 117–132. 1936.
20. ——— and Y. Chizaki. Cytological studies on genus hybrids among *Triticum*, *Secale*, and *Aegilops*. Jap. Jour. Bot. **7:** 1–32. 1934.
21. Katayama, Y. Karyogenetic studies on X-rayed cells and their derivatives in *Triticum monococcum*. Jour. Coll. Agr., Tokyo Imp. Univ. **13:** 397–414. 1935.
22. Kattermann, G. Die cytologische Verhältnisse einiger Weizenroggenbastarde und ihrer Nachkommenschaft ("F_2"). Züchter **6:** 97–107. 1934*a*.
23. ———. Zytologische Notiz über Weizenroggenbastarde. Zeits. Zücht. A. **19:** 183–194. 1934*b*.
24. ———. Die Paarungsintensität der Chromosomen bei Weizen-Roggenbastarden zweiter Generation in Vergleich zum Weizenelter. Planta **24:** 66–77. 1935.
25. ———. Genetische Ergebnisse bei Weizenroggenbastarden bei F_4. Mitteilung I: Die Behaarung des Holmes und Beziehungen dieses

Merkmals zu Strohlange und Bekörnung. Pflanzenbau **4**: 131–149. 1935.

26. ————. Zur Cytologie holmbehaarter Stamme aus Weizenroggenbastardierung. Züchter **9**: 196–199. 1937.
27. ————. Das Verhalten des Chromosoms für Behaarung roggenbehaarte Nachkommen aus Weizenroggenbastardierung in neuen Kreuzung mit Roggen und Weizen. Zeits. Ind. Abs. Ver. **74**: 1–16. 1937.
28. ————. Über konstante halmbehaarte Stamme aus Weizenroggenbastardierung mit $2n = 42$ Chromosomen. Zeits. Ind. Abst. Ver. **74**: 354–375.
29. KIHARA, H. Cytologische und genetische Studien bei wichtigen Getreidearten. Mem. Coll. Sci. Kyoto. Imp. Univ. B. **1**: 1–200. 1924.
30. ————. Ein diplo-haploides Zwillungspaar bei *Triticum durum*. Agr. & Hort. **11**: 1425–1434. 1936.
31. KOSTOFF, D. Chromosome behavior in *Triticum* hybrids and allied genera. II. Tr. Timopheevi ($n = 14$) × Secale cereale ($n = 7$). Zeits. Zücht. A. **21**: 378–379. 1937.
32. ————. [Frequency of polyembryony and chlorophyll deficiency in rye]. Compt. Rend. Acad. Sci. [Paris] **24**: 479–482. 1939.
33. KRISHNASWAMY, N. Cytological studies of a haploid plant of *Triticum vulgare*. Hereditas **25**: 77–86. 1939.
34. LEBEDEFF, V. N. The new phenomena in wheat-rye hybrids. Ukrain. Wiss. Forsch. Zückerind. 1–84. 1932.
35. ————. [The phenomena of autosyndesis in the interspecific hybrids of *vulgare* wheat and their significance in the problem of phylogenesis of wheat]. U.S.S.R. Narog. Komm. Snob. 1933*a*.
36. ————. [The new cases of formation of amphidiploids in wheat-rye hybrids]. U.S.S.R. Narog. Komm. Snob. 1933*b*.
37. LEDINGHAM, G. F., and W. P. THOMPSON. The cytogenetics of non-amphidiploid derivatives of wheat-rye hybrids. Cytoiogia **8**: 377–397. 1938.
38. LEIGHTY, C. E., and J. W. TAYLOR. "Hairy-neck" wheat segregates from wheat-rye hybrids. Jour. Agr. Res. **28**: 567–576. 1924.
39. LEVAN, A. Studies on the meiotic mechanism of haploid rye. Hereditas **28**: 177–211. 1942.
40. LILIENFELD, F., and H. KIHARA. Genom Analyse bei *Triticum* und *Aegilops*. Cytologia **6**: 87–122. 1934.
41. LILJEFORS, S. Zytologische Stüdien über den F_1 Bastard *Triticum turgidum* × *Secale cereale*. Hereditas **21**: 240–262. 1936.
42. LINDSCHAU, M., and E. OEHLER. Untersuchungen am konstant intermediären additiven Rimpauschen Weizen-Roggenbastard. Züchter **7**: 228–233. 1935.
43. LONGLEY, A. E., and W. J. SANDO. Nuclear divisions in the pollen mother cells of *Triticum*, *Aegilops*, and *Secale*, and their hybrids. Jour. Agr. Res. **40**: 683–719. 1930.
44. LOVE, H. H., and W. T. CRAIG. Fertile wheat-rye hybrids. Jour. Hered. **10**: 195–207. 1919.
45. MCCLINTOCK, BARBARA. The association of non-homologous parts of chromosomes in the mid-prophase of meiosis in Zea mays. Zeits. Zellf. & Mikr. Anat. **19**: 191–237. 1933.
46. MCFADDEN, E. S., and E. R. SEARS. The artificial synthesis of *Triticum spelta*. Rec. Gen. Soc. Am. **13**: 26–27. 1944.
47. ———— and ————. The origin of *Triticum spelta* and its free threshing and hexaploid relatives. Jour. Hered. **37**: 81–89, 107–116. 1946.
48. MEISTER, G. K. Natural hybridization of wheat and rye in Russia. Jour. Hered. **12**: 467–470. 1921.

49. ————. The principal results in the study of wheat-rye hybrids. Jour. Exp. Landw. Sudoest. Ruszl. S: 121–130. 1926.
50. ———— and N. MEISTER. Wheat-rye hybrids. Contr. Saratow. Agr. Exp. Sta. **1924:** 1–216. 1924.
51. MEISTER, N. G. Rye wheat hybrids and their importance in breeding. Selek. Semenov. **2:** 34–36. 1936.
52. ———— and N. A. TJUMJAKOFF. Rye-wheat hybrids and reciprocal crosses. Jour. Genet. **20:** 233–245. 1928.
53. MELBURN. M. Heterotypic prophases in the absence of chromosome pairing. Canad. Jour. Res. C. **1:** 512–527. 1929.
54. ————. Heterotypische Kernteilung des Weizenroggenbastarde. Biol. Zentralbl. **16:** 337–. 1930.
55. MIEGE, E. Sur les qualités boulangères des *Triticum* des *Aeglilops*, et de leurs hybrides. Compt. Rend. Acad. Sci. [Paris] **205:** 1435–1437. 1937.
56. MÜNTZING, A. Über die Entstehungsweise 56-chromosomiger Weizen-Roggen-Bastarde. Züchter **8:** 188–181. 1936.
57. ————. Note on a haploid rye plant. Hereditas **23:** 401–404. 1937.
58. ————. Studies on the properties and the ways of production of rye-wheat amphidiploids. Hereditas **25:** 387–430. 1939.
59. NAVALIKHINA, N. K. Restitution of fertility in a wheat-rye hybrid through colchicine treatment. Compt. Rend. Acad. Sci. [URSS] **27:** 587–589. 1940.
60. NIKOLAJEWA, A. G. The cytology of rye-wheat hybrids. Nauk. Agron. Zhur. **1:** 570–576. 1924.
61. NORDENSKIOLD, H. Studies of a haploid rye plant. Hereditas **25:** 204–210. 1939.
62. OEHLER, E. Untersuchungen über Ansatzverhältnisse, Morphologie, und Fertilität bei Weizen-Roggenbastarden. Zeits. Zücht. A. **16:** 357–393. 1931*a*.
63. ————. Die Ausnützung von Species- und Gattungs-kreuzungen in der Weizen und Roggenzüchtung. Zeit. Ind. Abst. Ver. **57:** 363–369. 1931*b*.
64. O'MARA, J. G. Fertility in allopolyploids. Rec. Gen. Soc. Am. **17:** 52. 1948.
65. ————. Cytogenetic studies on Triticale. II. The kinds of intergeneric chromosome addition. Cytologia **16:** 225–232. 1951.
66. PAREMUD, L. K. New forms of wheat-rye hybrids. Selek. Semenov. **4:** 4–5. 1940.
67. PLOTNIKOV, T. V. Forms with high chromosome numbers in the progeny of the wheat-rye hybrids. Arb. Cyt. Lab. Wiss. Inst. Select **2:** 203–208. 1927.
68. ————. Zytologische Untersuchungen von Bastarden zwischen 28 chromosomigen Weizen und Roggen. Planta **12:** 167–183. 1931.
69. PLOTNIKOWA, T. W. Zytologische Untersuchungen an hyperchromosomigen Weizen-Roggen-Bastarden. Zeits. Ind. Abst. Ver. **66:** 404–424. 1933.
70. RAW, A. R. Genetical studies with wheat haploids of *Triticum vulgare*. Jour. Rep. Agr. Victoria **35:** 300–306. 1937.
71. RIMPAU, W. Kreuzungsprodukte landwirtschaftliche Kulturpflanze. Landwirt. Jahrb. **20:** 335–371. 1891.
72. ROSENSTIEL, K. v. Über Weizen-Roggen-Bastarde. Forschungsdienst. Sonderheft **10:** 63–76. 1938.
73. SAKAMURA, T. Kurze Mitteilung über die Chromosomenzahlen und die Vervandtschaftsverhältnisse der Triticum-Arten. Bot. Mag. Tokyo **32:** 151–154. 1918.
74. SAMOCHWALOW, G. K. Analysis of certain chemical characters of rye-wheat hybrids and their parental forms. Chem. Soc. Agr. **8:** 85–90. 1935.

75. SAX, K. Sterility in wheat hybrids. II. Chromosome behavior in partially sterile hybrids. Genetics **7:** 513–552. 1922.
76. SCHIEMANN, E. New results in the history of cultivated cereals. Heredity **5:** 305–320. 1951.
77. SEARS, E. R. Cytogenetic studies with polyploid species of wheat. I. Chromosomal aberrations in the progeny of a haploid of *Triticum vulgare*. Genetics **24:** 509–523. 1939.
78. ————. Nullisomics in *Triticum vulgare*. Genetics **26:** 167–168. 1941.
79. ————. Cytogenetic studies with polyploid species of wheat. II. Additional chromosomal aberrations in *Triticum vulgare*. Genetics **29:** 232–246. 1944.
80. ————. The cytology and genetics of the wheats and their relatives. Adv. Genet. **2:** 239–270. 1948.
81. ————. Homeologous chromosomes in *Triticum aestivum*. Rec. Gen. Soc. Am. **21:** 68. 1952.
82. SMITH, L. Haploidy in einkorn. Jour. Agr. Res. **73:** 291–301. 1946.
83. TAKAGI, F. Karyogenetical studies on rye. I. A trisomic plant. Cytologia **6:** 496–501. 1935.
84. TAYLOR, J. W. Irregularities in the inheritance of the hairy neck character transposed from *Secale* to *Triticum*. Jour. Agr. Res. **48:** 603–617. 1934.
85. THOMPSON, W. P. Chromosome behavior in a cross between wheat and rye. Genetics **11:** 317–332. 1926.
86. ————. Chromosome homologies in wheat, rye, and *Aegilops*. Canad. Jour. Res. C. **4:** 624–634. 1931.
87. TOMETORP, G. Cytological studies on haploid *Hordeum distichum*. Hereditas **25:** 241–254. 1939.
88. TSCHERMAK, E. Weizen-Roggen-Bastarde und ihre züchterische Verwertung. Züchter **3:** 244–248. 1931.
89. TSCHERMAK-SEYSENEGG, E. Wirkliche, abgeleitete, und fragliche Weizenroggenbastarde (Triticale-Formen). Cytologia, Fujii Jub. Vol.: 1003–1011. 1937.
90. ————. Beiträge zur züchterischen und zytologischen Beurteilung der Weizen-Roggen-und Weizen-Quecken-Bastarde. Zeits. Zücht. A. **22:** 397–416. 1938.
91. UPCOTT, M. The external behaviour of the chromosomes. VI. The behaviour of the centromere at meiosis. Proc. Roy. Soc. B. **124:** 336–361. 1937.
92. VAKAR, B. A. Cytological study of constant wheat-rye hybrids. Trudy Omsk Inst. Sel Khoz. **1:** 59–103. 1935.
93. ———— and KROT, E. G. A cytological study of constant wheat-rye hybrids. Cytologia **5:** 395–416. 1934.
94. VASILIEV, B. Wheat-rye hybrids. II. Genetical analysis of cross-ability of rye with various species of wheat. Compt. Rend. Acad. Sci. [U.R.S.S.] **27:** 598–600. 1940.
95. WILSON, A. S. On the fertilisation of the cereals. Trans. Proc. Bot. Soc. Edinburgh **12:** 84–96. 1874.
96. ————. On the fertilisation of the cereals. Trans. Proc. Bot. Soc. Edinburgh **12:** 237–242. 1875.
97. ————. On wheat and rye hybrids. Trans. Proc. Bot. Soc. Edinburgh **12:** 286–288. 1876.
98. YAMASAKI, Y. Cytological studies on haploid wheat plants. Jap. Jour. Genet. **11:** 314–315. 1935.
99. ————. Some observations on the microsporogenesis of the haploid plant of *Triticum vulgare* Host. Jap. Jour. Bot. **8:** 151–153. 1936.
100. ZALENSKY, V. R., and A. V. DOROSHENKO. Zytologische Untersuchungen bei Weizenroggenbastarden. Bull. Appl. Bot. **14:** 185–210. 1925.

DISEASE RESISTANCE IN THE VEGETABLE CROPS. II[1]

J. C. WALKER
Department of Plant Pathology, University of Wisconsin

Twelve years ago the writer assembled the information available at that time on the nature of disease resistance and on the development of resistant varieties in vegetable crops. The amount of progress in the past decade is ample evidence that attention to this important phase of plant disease control has increased steadily. The present review is an appendix to that published in 1941, and the material is again arranged under the various crops concerned.

GARDEN BEAN

ANTHRACNOSE (*Colletotrichum lindemuthianum* (Sacc. & Magn.) Briosi & Cav.). Further studies on the inheritance of anthracnose resistance was reported by Andrus and Wade (21). A new race, *delta,* was described from North Carolina. Fifteen parent varieties and selections differing in reaction to races *beta, gamma* and *delta* were used. In resistant × tolerant and in resistant × susceptible crosses, resistance to *beta* was dominant. In crosses of tolerant × susceptible, susceptibility was dominant. When *gamma* and *delta* races were considered, a system of ten genes in three allelomorphic series, involving both duplicate and complementary genes for resistance, one dominant gene for susceptibility, and gene interactions at three points, was the simplest Mendelian hypothesis coordinating all the data.

Yu (260) found the pathogen isolated from broad bean (*Vicia faba* L.) in China to be non-pathogenic on *Phaseolus vulgaris,* indicating it to be a distinct race of *C. lindemuthianum.*

COMMON BACTERIAL BLIGHT (*Xanthomonas phaseoli* (E.F.Sm.) Dows.) and HALO BLIGHT (*Pseudomonas phaseolicola* (Burk.) Dows.). Burkholder and Bullard (50) in New York studied the reaction of 40 varieties and strains of bean to fuscous blight incited by *X. phaseoli fuscans* (Burk.) Starr & Burk. They found U.I.

[1] Supplement to article in The Botanical Review 7: 458–506. 1941.

Great Northern No. 1 resistant and suggested it as a breeding parent. Working with halo blight, Jensen and Goss (112) in Nebraska found Red Mexican, Schwert 27 and Schwert Nordstern highly resistant. Other varieties studied varied in degrees of stem, leaf and pod susceptibility. Mastenbroek (134) in Holland listed Blanca, of Dutch origin, and Robust, Cornell 22, U.I. Great Northern 81, 123, 139, Japanese White, Michelite and Michigan White as resistant to halo blight. According to Zaumeyer and Thomas (266), no snap or dry bean varieties grown in the United States are highly resistant to common blight. Pinto, Great Northern, Red Mexican and pea types of dry beans and some pole and semi-pole snap bean varieties are fairly tolerant of halo blight, but none may be regarded as highly resistant

RUST (*Uromyces phaseoli typica* Arthur). Harter and Zaumeyer (90) demonstrated 20 physiologic races of the pathogen in 1941. In 1952 Fisher (72) reported ten new races collected chiefly in the Rocky Mountain States. Zaumeyer and Harter (263) studied the inheritance of resistance to six races. Resistance to races 1 and 2 was governed by a single dominant gene. Other genetic factors appeared to influence the expression of resistance to races 6, 11, 12 and 17. Modifying factors may be responsible for variation in resistance found within major classes set up for resistance and susceptibility. This might account for the fact that in F_2 progenies inoculated with race 11, one quarter of the plants were more resistant than the resistant parent. F_3 progenies from intermediate F_2 plants inoculated with race 17 segregated into three resistant to one susceptible when the environment was relatively unfavorable for the disease, whereas when the tests were run in a more favorable environment they segregated at the ratio of one resistant to two intermediate to one susceptible. In 1946 Zaumeyer and Harter (265) announced two new varieties, Pinto No. 5 and Pinto No. 14, which were resistant to 22 of the 24 races they recognized at that time. These varieties are also tolerant of common mosaic and of halo blight. They were both derived from a cross between Idaho Pinto (early, rust-susceptible) and resistant white-seeded Kentucky Wonder. Townsend and Wade (217) developed Florida Belle and Florida White Wax which were resistant to some forms of rust prevalent in Florida. Frazier and Hendrix (76) in 1949 announced a new pole green bean (Hawaiian Wonder), derived

from a cross between Bountiful and Lualualei, which was resistant in Hawaii at high elevations where rust is a limiting factor. Wellhausen et al. (242) in 1949 introduced Rocamex 1, 2 and 3 for cultivation in the central plateau of Mexico where they were resistant to the races which prevailed there. Westralia is a pole variety developed in Australia (53).

POWDERY MILDEW (*Erysiphe polygoni* DC.). Dundas (65, 66) reported further studies on the inheritance of resistance to race 1 of the pathogen, using the detached leaf test along with field inoculation. He found the same dominant gene for resistance in several varieties. Pink, which also presumably contained the same gene, was susceptible in the early stages of disease development, but leaves became resistant as they approached maturity. Long Roman, which showed an intermediate degree of resistance in the field, was susceptible in the detached leaf test, and its breeding behavior showed it to be homozygous for the recessive susceptibility gene. The main dominant factor for resistance was effective against 12 of 14 races isolated and tested. Florida Belle and Florida White Wax varieties are new introductions resistant to some strains of mildew (217). Zaumeyer and Thomas (266) in 1949 listed the following varieties as generally only slightly susceptible: Logan, Ranger, Idaho Refugee, Sensation Refugee Nos. 1066 and 1071 (16), Rival, Topcrop, Blue Lake, Blue Lake Stringless, Kentucky Wonder and White Kentucky Wonder.

VIRUS DISEASES. Our knowledge of the genetics of resistance to typical bean virus 1, the incitant of common bean mosaic, has been advanced markedly by Ali (15). Until the present time resistance has been derived from one of three sources: Corbett Refugee, Robust and Great Northern. Idaho Refugee and U.S. No. 5 Refugee (derived from Corbett Refugee) and Robust were used as resistant parents in crosses with susceptible Stringless Green Refugee. When Idaho Refugee and U.S. No. 5 were used, resistance was dominant in the F_1 and segregation in the F_2 was three resistant to one susceptible. When Robust was used, susceptibility was dominant and segregation in the F_2 was three susceptible to one resistant. When the two resistant parents, Robust and U.S. No. 5, were crossed, the F_1 was resistant, but in the F_2 segregation was 13 resistant to three susceptible. Grogan and Walker (86)

had shown previously that when U.S. No. 5, Idaho Refugee and Robust were inoculated by the approach-graft technique, the two parental types reacted quite differently. U.S. No. 5 and Idaho Refugee were extremely hypersensitive and developed phloem necrosis followed by top necrosis and death, whereas Robust showed no evidence of virus infection. When the F_2 progeny of U.S. No. 5 × Robust was tested by this technique, the resistant plants were divided at the rate of nine top-necrotic like the U.S. No. 5 parent to four symptomless like the Robust parent. The F_3 families, inoculated by the standard method, were distributed in the following ratio: seven symptomless; four segregating, 13 healthy to three diseased; two segregating, three healthy to one diseased; two segregating, one healthy to three diseased; one all diseased. On the basis of these data Ali postulated two gene pairs. *A* is a dominant gene for susceptibility which permits virus infection and disease development; *a*, the recessive to *A*, confers resistance to infection and consequently to top necrosis. *I* in combination with *A* prevents infection after rubbing inoculation and commonly in field exposure to insect vectors but does not prevent virus increase and the hypersensitive reaction in the phloem when a continuous supply of virus is provided by the approach-graft technique; *i*, the allele of *I*, has no influence on infection and subsequent development. The genotypes of the four varieties studied were thus as follows:

Stringless Green Refugee, *AAii*, susceptible.
U.S. No. 5 Refugee, *AAII*, resistant but top-necrotic.
Idaho Refugee, *AAII*, similar to U.S. No. 5.
Robust, *aaii*, resistant but not top-necrotic.

Wade and Andrus (221) found a single-factor difference between U.S. No. 5 Refugee and Stringless Black Valentine, indicating that the latter has the genotype *AAii*. Numerous varieties are now known to be resistant to typical common mosaic. Recent lists are given by Zaumeyer and Thomas (262, 266).

In 1943 Richards and Burkholder (176) described a virus in New York which resembled bean virus 1 in that it was seed-borne and noninfectious on Corbett Refugee and Idaho Refugee but infectious on Robust. What appears to be the same virus was described by Dean and Hungerford (63) in Idaho in 1946. This is now regarded as a strain of bean virus 1. While many snap bean

varieties are resistant to both the typical and atypical strain, many of the currently used dry bean varieties are resistant to the typical strain but susceptible to the atypical strain.

Zaumeyer and Harter (264) showed that many varieties of bean developed only local lesions on inoculated leaves and were otherwise resistant to bean virus 4 which incites southern mosaic. This character is dominant over susceptibility and is controlled by a single gene pair. Reaction to the pod mottle virus was shown by Thomas and Zaumeyer (211) to follow the same pattern of inheritance.

At the Idaho station, breeding work has continued in which resistance to common mosaic is being combined with resistance to curly top (101, 151). The first double resistant varieties introduced were Red Mexican U.I. 3 and 34. Great Northern double resistant varieties now include G.N. U.I. 15, 16 and 31. From a cross between U.I. 34 and Pinto the following double resistant Pinto types have been developed: Pinto U.I. 72, 78 and 111. Schultz and Dean (194) found resistance to curly top to be dominant, and inheritance studies indicated that two gene pairs were involved.

LIMA BEAN

MOSAIC. In 1936 Harrison (89) reported five varieties of lima bean which were free from mosaic symptoms and five which had 95 to 100 per cent of the plants affected in a trial at Geneva, New York. In 1946 Pryor and Wester (169) noted a similar difference at Beltsville, Maryland, where one new variety U.S. 343 was severely diseased, while another, U.S. 243, was free from symptoms. In 1951 Thomas, Zaumeyer and Jorgensen (212) reported a study of the inheritance of resistance. In crosses between Fordhook (resistant) and Sieva (susceptible) resistance in the F_1 was completely dominant. Analysis of the reaction of F_2 and F_3 progenies led them to conclude that resistance was controlled by two dominant complementary genes.

DOWNY MILDEW (*Phytophthora phaseoli* Thaxt.). Thomas, Jorgensen and Wester (210) found resistance in four accessions from 113 tested. Very little sporulation of the pathogen occurred on plants from these lines in the field and after artificial inoculation in the greenhouse. Resistance is controlled by a single dominant gene.

CELERY

Wilson (254) published valuable data on the relative resistance of many commercial varieties of celery to yellows (*Fusarium oxysporum* f. *apii* (R. Nelson & Sherb.) Snyder & Hansen). Resistant varieties of the golden type developed at Cornell University were released as Cornell 6 and Cornell 19. A new yellows-resistant variety of the light green type was released by Nelson (152) at Michigan Experiment Station as Michigan State Green-Gold.

Townsend, Emerson and Newhall (216) found seven varieties of Turkish origin highly resistant to early blight (*Cercospora apii* Fres.). Equally good resistance was also found in a Danish variety with hollow petioles. From a cross between the Danish variety and Golden Self-Blanching followed by crosses to yellows-resistant Cornell 6 and Cornell 19, a line of the green petiole type was secured which was moderately resistant to early blight and to late blight (*Septoria apii-graveolentis* Dorogin) and highly resistant to yellows. From this program the variety Emerson Pascal was released by Munger and Newhall (150).

Pope, Munger and Carew (159) reported that susceptibility to chlorosis induced by magnesium deficiency is a recessive character controlled by a single gene.

CRUCIFEROUS VEGETABLES

BLACK ROT (*Xanthomonas campestris* (Pam.) Dows.). Observations on the resistance of seedlings of varieties and species of *Brassica* were reported by Bain (25). He noted that, when plants were inoculated by dipping seed in a suspension of the bacteria before sowing, turnips and mustards as a group were lower in disease incidence than varieties of the Cole group. Within the latter, however, varieties differed widely in disease incidence. Progenies from healthy survivors indicated that resistance could be improved by selection within commercial varieties. Thung (214*a*) in Indonesia reported several moderately resistant varieties of cabbage.

WHITE RUST (*Albugo candida* (Pers. ex Chev.) Kuntze). Hougas, Rieman and Stokes (99) succeeded in obtaining hybrids between commonly grown, male-sterile horseradish and certain clones of the smooth-leafed Bohemian type which is highly resistant to white rust. Of 169 hybrid seedlings, four were similar to Bohemian in resistance and three were even more resistant than the

latter. This work opens the possibility of developing satisfactory common clones with resistance to this important disease of horseradish.

CABBAGE YELLOWS (*Fusarium oxysporum* f. *conglutinans* (Wr.) Snyder and Hansen. Resistant varieties available up to 1948 are described by Walker (222), Walker and Jolivette (225), and Walker, Larson, Foster and Kuntz (229).

RADISH WILT (*Fusarium oxysporum* f. *raphani* Kendr. & Snyder). This form and form *conglutinans* may both infect radish (22). Pound and Fowler (167) have reported progress in the selection of wilt-resistant strains of radish.

CABBAGE CLUBROOT (*Plasmodiophora brassicae* Wor.). Walker and Larson (227, 228) found resistance in a kale-cabbage hybrid rogue. This was used as a parent for crossing and backcrossing to cabbage. Resistance is recessive and appears to be controlled by the combined action of several genes. While no resistant varieties have been released, substantial progress is being made in combining clubroot resistance and yellows resistance with commercially acceptable horticultural types. Gante (78*a*) in Germany reported two resistant varieties, Böhmerwald and Bindsachsener.

CABBAGE MOSAIC. This disease is usually incited by combined infection by turnip virus 1 and cauliflower virus 1. Pound (164) studied the relative resistance of a number of standard cabbage varieties. He found that although in all cases the viruses increased in inoculated plants, the varieties represented a distinct gradient as to resistance and also that variation among individuals often occurred within a variety. The varieties he studied fell roughly into three classes, the most resistant group containing Wisconsin All Seasons, Stein's Early Flat Dutch, All Head Select, Succession and Globe. Walker and Pound (231) developed a more uniform horticultural type in Wisconsin All Seasons by selection and at the same time increased the level of resistance. This line in which yellows resistance and mosaic resistance are combined was released as Improved Wisconsin All Seasons. Pound and Walker (168) studied the inheritance of mosaic resistance. They found that relatively high degree of resistance can be secured by selection within most, if not all, cabbage varieties. In crosses between resistant lines derived from different varieties, the level of resistance of both par-

ents was maintained. Resistance to the mottle symptom induced by turnip virus 1 and to the chlorosis symptom induced by cauliflower virus 1 are in each case incompletely dominant, and both types are inherited as quantitative characters. In a study of the relation of air temperature to concentration of turnip virus 1 and resistance in the greenhouse, Pound (165) noted that plants of highly resistant lines expressed resistance only at 24° C and below. There was a close correlation between symptom severity and virus concentration.

CUCURBITS

FUSARIUM WILT OF WATERMELON (*Fusarium oxysporum* f. *niveum* (E.F.Sm.) Snyder & Hansen). Wilt-resistant varieties developed in the past ten years include Blacklee (233), Ironsides (157), Miles (69, 70), Black Kleckley (157) (also resistant to anthracnose), Georgia Wilt-Resistant (218), Missouri Queen (157), Brownlee (157), Improved Leesburg (157), Wilt-Resistant Dixie Queen (157), and Baby Klondike (62). Welch and Melhus (241) announced an F_1 hybrid between a wilt-resistant inbred and susceptible Dixie Queen. They and Parris (155) found wide differences in the F_1 reaction of various resistant × susceptible crosses. Braun (46) found more acetic acid in resistant citron than in susceptible watermelon, but its relation to the resistant character was not demonstrated.

FUSARIUM WILT OF MUSKMELON (*Fusarium oxysporum* f. *melonis* (Leach & Currence) Hansen & Snyder). Three wilt-resistant varieties have been released. Golden Gopher was developed at the Minnesota Experiment Station. Iroquois (148) and Delicious 51 were produced at Cornell University. The latter variety was developed from a cross between Iroquois and Delicious followed by four backcrosses to Delicious; it is earlier than Iroquois.

SCAB OF CUCUMBER (*Cladosporium cucumerinum* Ell. & Arth.). In addition to Maine No. 2 reported earlier, another variety, Highmoor, a slicing type, has been released by the Maine Experiment Station. Walker (223) confirmed an earlier report by Bailey that resistance in cucumber is controlled by a single dominant gene. He showed that homozygous and heterozygous resistant plants could be detected reliably in the early seedling stage by inoculating and

holding in a moist chamber for several days at approximately 17° C. At 22° and above, susceptible plants cicatrized the fungus lesions and could not be readily distinguished from resistant ones. Two new varieties, Wisconsin SR 6 and Wisconsin SR 10, were released in 1952 by the Wisconsin Experiment Station (230, 232). Wisconsin SR 6 was developed by crossing Maine No. 2 with National Pickling and backcrossing to the latter for three successive generations. It conforms to National Pickling in type. Wisconsin SR 10 was developed from a cross of the first backcross with National Pickling with Chicago Pickling followed by two backcrosses with Chicago Pickling. It resembles the latter in type.

POWDERY MILDEW (*Erysiphe cichoracearum* DC.). In further breeding work in southern California to secure a cantaloupe resistant to race 1 and race 2, greenhouse screening techniques to supplement field tests were developed by Pryor and Whitaker (170). A strain highly resistant to race 1 and race 2 was obtained from the same source material from which cantaloupe No. 45 (resistant only to race 1) was derived. Whitaker and Pryor (251, 252, 253) reported that resistance to race 2 was intermediate in the F_1. With this new parental material Whitaker and Davis (249) developed and released cantaloupes No. 6 and No. 7 which are highly resistant to race 1 and race 2. Van Haltern (219) in 1951 introduced Georgia 47 cantaloupe which is resistant to both powdery and downy mildew.

Smith (198) noted that Puerto Rico 37 cucumber is highly resistant to powdery mildew. Studies of a cross with a susceptible variety indicated that resistance was polygenic in inheritance.

CUCUMBER MOSAIC (*Cucumber virus* 1). Chinese Long and Tokyo Long Green varieties of cucumber are highly resistant to mosaic. They have been used as parental stocks in the development of resistant varieties of commercial value in the United States. Wilson and Wilson (258) developed Ohio 31 from a cross between Tokyo Long Green and National Pickling. Several other varieties highly resistant to mosaic are now in general use. Yorkstate Pickling was developed at Cornell University by Munger (149) from a cross between Chinese Long and Early Russian followed by three crosses with National Pickling. From the first backcross with the latter Wilson (256), in cooperation with O. S. Cannon and C. A.

John of the H. J. Heinz Co., developed Ohio MR 17. Munger (149) developed a mosaic-resistant slicing variety, Niagara, from a cross between a resistant strain developed by O. H. Elmer of the Kansas Agricultural Experiment Station and Cubit. Shifriss, Myers and Chupp (197) studied inheritance of mosaic resistance, using Chinese Long, Tokyo Long Green and Shamrock as resistant parents. One phase of the disease, chlorosis of inoculated cotyledons, appears to be controlled by three complementary genes. The extent of systemic symptoms is determined by dominant modifiers.

WATERMELON ANTHRACNOSE (*Colletotrichum lagenarium* (Pass.) Ell. & Halst.). It was pointed out in the last report that resistance to anthracnose is controlled by a single dominant gene. Two new varieties, Congo and Black Kleckley, which are highly resistant to anthracnose, are now in use (157). The latter variety is also resistant to Fusarium wilt.

DOWNY MILDEW (*Pseudoperonospora cubensis* (Berk. & Curt.) Rostow.). In the last report it was stated that resistance to downy mildew in cucumber had been found in Puerto Rico in stocks imported from China. From a cross between Puerto Rico 40 and Cubit, Barnes (26) in South Carolina developed a new partially resistant slicing variety introduced as Palmetto. Another variety from the same source is Santee (27). Jenkins (109, 110) studied the inheritance of mildew resistance. It appears to be a polygenic character. The expression of resistance is influenced by the stage of host development at time of infection (29).

Ivanoff (108) in Texas found four cantaloupe varieties of West Indian origin to be highly resistant. Using some of them as resistant parents, he developed Texas Resistant No. 1. Georgia 47, developed at the Georgia Experiment Station by Van Haltern (219), and Rio Sweet, developed at the Texas Experiment Station by Godfrey (83), are more recent and more widely used varieties. Parris (156) in Florida reported strains of watermelon from the Dominican Republic which were highly resistant to downy mildew and useful as parents in watermelon improvement.

CERCOSPORA LEAF SPOT OF CUCUMBER (*Cercospora melonis* Cke.). This disease is important on cucumbers grown under glass in Europe. Early in the century it almost completely destroyed the

crop in the area north of London. Butcher's Disease Resister is highly resistant and is now used widely (139). This variety and Spot Resisting are the only ones found to be highly resistant in tests of 37 commercial varieties conducted by Klimke (119) in Germany. Penetration of resistant plants occurs, but the pathogen is inhibited from further growth before it causes any perceptible injury.

LETTUCE

Varieties of head lettuce developed by the U. S. Department of Agriculture in commercial use in 1951 were described by Bohn and Whitaker (42). All are highly resistant to brown blight. Of those described, Imperial 456 and Great Lakes are highly resistant to tipburn. Several of the varieties are highly resistant to some physiologic races of *Bremia lactucae* Reg., the downy mildew pathogen, but each is susceptible to one or more races. In a study of inheritance of resistance to powdery mildew (*Erysiphe cichoracearum* DC.), Whitaker and Pryor (250) found resistance in Imperial 850 to the race of the fungus concerned to be controlled by a single dominant gene. Thompson (213) observed two strains each of *Lactuca serriola* and *L. saligna* which showed high percentages of plants which escaped infection by the aster yellows virus. Barnes (28) introduced in 1951 a mosaic resistant cos variety adapted to North and South Carolina under the name Parris Island.

ONION

The relation of disease resistance to onion breeding is discussed by Jones (114).

SMUDGE (*Colletotrichum circinans* (Berk.) Vogl.) and NECK ROTS (*Botrytis allii* Munn; *B. byssoidea* J. C. Walker; and *B. squamosa* J. C. Walker). One type of resistance is associated with bulb pigment. The interpretation of inheritance of pigment and of resistance earlier reported by Rieman (178) has been modified by the work of Clarke, Jones and Little (55). Rieman demonstrated two kinds of factors for white (susceptible), one an incompletely dominant inhibitor (*I*), the other a white factor recessive to red and to yellow. He regarded red, yellow and white as an allelomorphic series. Clarke et al. showed yellow and red to be allelomorphs, but not white. A dominant allele *C* is necessary for color

development. A homozygous red has the genotype *iiCCRR;* a homozygous yellow is *iiCCrr;* a recessive white is *iiccRR, iiccRr* or *iiccrr*. The *I* gene is incompletely dominant and in the heterozygous condition in combination with CCRR, i.e., *IiCCRR* produces an intermediate pink color, while the genotype *IiCCrr* is cream rather than yellow. Jones et al. (117) studied the influence of the gene pair *Ii* on resistance to smudge. In F_1 progenies from *IICCrr* (white, susceptible) and *iiCCrr* (yellow, resistant), the cream hybrids showed a disease index approximately intermediate between those of the two parents.

While the resistant factor has been shown to consist of colorless phenolic substances, principally protocatechuic acid and catechol, associated with pigment metabolism, it has long been known that volatile substances, principally allyl sulfides, present in fleshy scales are also antibiotic to smudge and neck rot organisms. Hatfield, Walker and Owen (93) and Owen, Walker and Stahmann (154) have studied this factor further in relation to resistance. In a comparison of mildly pungent and strongly pungent varieties in white, yellow and red classes, they demonstrated that the pungent factor had a secondary influence on resistance to smudge. Whereas all white varieties were very susceptible in comparison with red and yellow varieties, white strongly pungent varieties were slightly more resistant than white mildly pungent varieties. Red and yellow varieties were highly resistant, but the mildly pungent varieties in each color class were slightly less so than strongly pungent ones. In *IiCCrr* hybrids the disease index deviated from the mean of the two parents toward that of the yellow parent when both parents were strongly pungent, while it deviated in the direction of the white parent when both parents were mildly pungent.

In the case of neck rot resistance the pungent factor was primary, whereas the color factor was secondary. Under most favorable conditions for penetration there was no significant difference between white and colored varieties, but within each color class the strongly pungent varieties were significantly more resistant than the mildly pungent varieties. Under less favorable conditions for penetration, colored varieties were significantly more resistant than white varieties, but within each color class the strongly pungent varieties were again more resistant than mildly pungent ones. This difference in resistance to smudge and neck rot was attributed to

the difference in threshold of infection in the two diseases. In smudge the pathogen penetrates directly into the outer scale and necessarily comes into immediate contact with the phenols. In neck rot the pathogen penetrates chiefly through the wounded neck tissue where the chances of contact with the phenols are much smaller and the pungency factor consequently becomes the more influential.

As yet no success has been had in breaking the close association between color and resistance. Presumably formation of the phenols and of the pigments is controlled by the same genes, or the linkage is extremely close.

DIPLODIA ROT (*Diplodia natalensis* Pole-Evans). Ramsey, Heiberg and Wiant (171) reported this disease to be confined to white varieties. They concluded that the same phenol factor described above for smudge was responsible for resistance in colored varieties.

BLACK MOLD (*Aspergillus niger* v. Tiegh.). Although this pathogen attacks outer bulb scales in much the same relation as the smudge pathogen, no correlation between resistance and color has been noted. In fact Hatfield et al. (93) and Owen et al. (154) showed that under some conditions, colored varieties are more severely affected than white ones. In some cases a water extract of outer colored scales stimulated germination and growth of *A. niger*. Thus it is indicated that the same phenol factor which contributes resistance to smudge, neck rots and *Diplodia* rot, contributes susceptibility to black mold.

PURPLE BLOTCH (*Alternaria porri* (Ell.) Cif.). Riollano (180) reported Louisiana Red Creole variety resistant in Puerto Rico.

PINK ROOT (*Pyrenochaeta terrestris* (Hansen) Gorenz, J. C. Walker and Larson). Gorenz, Larson and Walker (84) studied the effect of temperature and nutrient on disease incidence in young seedlings. They worked out a procedure in which breeding progenies can be tested in sand-nutrient culture under controlled sand temperature. By this method they showed a wide range of pathogenicity in various isolates, but all varieties tested responded in the same relative order of resistance to each isolate. Yellow Bermuda and Excel were the most resistant varieties of onion tested. Beltsville Bunching, an amphidiploid from a cross of onion and Welsh onion, was also highly resistant. Other resistant varieties are in

the process of development in the U. S. Department of Agriculture onion breeding program. Tims (215) reported a resistant variety of shallot, " Louisiana Pearl ", developed at the Louisiana Experiment Station.

Gasiorkiewicz, Larson, Walker and Stahmann (79) modified both morphology and pathogenicity of the pathogen by inducing mutations through the use of nitrogen mustard.

DOWNY MILDEW (*Peronospora destructor* (Berk.) Casp.). Jones, Porter and Leach (116) reported that the male sterile line of Italian Red, designated as 13-53, had high resistance of seed stalks and moderate resistance of foliage. Calred is the only commercial mildew resistant variety introduced so far. It is a fertile selection from 13-53 × Lord Howe Island. Warid and Tims (235) crossed Calred and susceptible Creole. Resistance was recessive. Segregation in F_2 progenies indicated that two gene pairs were involved.

SMUT (*Urocystis cepulae* Frost). Jones and Clarke (115) secured a fertile amphidiploid from a cross between resistant Welsh onion and susceptible onion. The amphidiploid was found by Walker, Jones and Clarke (226) to be nearly as resistant to smut as the Welsh onion parent. Since backcrosses to onion are highly self-sterile, no progress has been made in incorporating resistance in common onion.

YELLOW DWARF. Brierley and Smith (48) studied the reaction of onion varieties and Welsh onion to four isolates of the virus. Eight varieties of onion, Nebuka variety of Welsh onion, and an amphidiploid from Nebuka × White Portugal were highly resistant to isolates from onion, garlic and narcissus. All but the last two were susceptible to an isolate from shallot.

GARDEN PEA

WILT (*Fusarium oxysporum* f. *pisi* (Linford) Snyder & Hansen, race 1). Schroeder and Walker (192), by the use of sand cultures and a balanced nutrient solution, showed that the optimum root temperature for disease development was about 28° as compared with 21° when soil culture was used. With nutrient solution culture vascular invasion was greatest at 22°, but cortical root decay increased up to 28°. Under these atypical conditions resistant plants were affected much more severely than in soil culture. In

the past ten years many new wilt-resistant freezing and canning varieties have been developed, chiefly by seed-producing companies. The new list includes Teton, Glacier, Ranger, Bonneville, Early Perfection, Perfected Wales, Pride, Canner King, Freezonian, Wasatch, Shoshone, Mammoth Early Canner and Superior.

NEAR-WILT (*Fusarium oxysporum* f. *pisi* (Linford) Snyder & Hansen, race 2). Hare, Walker and Delwiche (87) produced a true-breeding resistant line by selection from a cross between two lines of Admiral. This was crossed with Pride, and from the cross a new variety, Delwiche Commando, was selected and released. Resistance was found to be controlled by a single dominant gene. A standardized technique was devised by Wells, Hare and Walker (246) for the testing of breeding material in the greenhouse. With the use of this technique Wells, Walker and Hare (247) showed that the gene for wilt resistance (*Fw*) and that for near-wilt resistance (*Fnw*) were associated with a loose linkage of 40.2 ± 3.4 per cent. Hagedorn of the Wisconsin Experiment Station released New Era in 1951. Derived from a cross between Delwiche Commando and Wisconsin Perfection, it is resistant to wilt, near-wilt and mosaic incited by bean virus 2.

ASCOCHYTA DISEASES (*Mycosphaerella pinodes* (Berk. & Blox.) Stone; *Ascochyta pinodella* L. K. Jones; *Ascochyta pisi* Lib.). While indications of some differences in resistance to the first two pathogens have been secured in Germany by Noll (153) and Stoll (208), there are as yet no varieties in American use which have resistance of any commercial value. Weimer (239, 240) tested many varieties in Georgia and found Austrian Winter field pea the most resistant. Wark (236) in Australia also found resistance to *Ascochyta pisi* to be highest in Austrian Winter. His inheritance studies indicated that it was controlled by the combined effect of three dominant genes. Hunter and White (102), Gilpatrick and Busch (82) in Canada, and Gerritsen and Burgmans (81) in Holland have reported varieties or strains resistant to *A. pisi*.

SEPTORIA BLOTCH (*Septoria pisi* West.). Zaumeyer (261) inoculated 134 pea varieties in the field in Colorado. One strain of Perfection and an accession from Puerto Rico were highly resistant.

POWDERY MILDEW (*Erysiphe polygoni* DC.). Harland (88) found about ten per cent of plants in a locally grown collection in

Peru resistant to mildew. Susceptibility was shown to be governed by a single dominant gene, *Er*. Pierce (158) in Montana found a selection from Stratagem highly resistant, resistance and susceptibility being also controlled by a single gene pair with susceptibility dominant. Whether or not the same gene pair was concerned in both instances has not been determined.

SPINACH

Smith (199) found high resistance to downy mildew (*Peronospora effusa* (Grev. ex Desm.) Ces.) in two accessions from Iran. The character was shown to be controlled by a single dominant gene.

Cook et al. (60) selected a strain from mosaic-resistant Virginia Savoy which is resistant to wilt (*Fusarium oxysporum* f. *spinaciae* (Sherb.) Snyder & Hansen).

Fulton (77) reported a strain of cucumber virus 1 to which the resistant varieties Virginia Savoy and Old Dominion were very susceptible. Pound and Cheo (166) found that the resistance of Virginia Savoy to the typical strain of the virus was expressed at 16° and 20° C, while at 28° the plants succumbed to systemic necrosis. Resistance appeared to be controlled by a single dominant gene.

SWEET POTATO

WILT OR STEM ROT (*Fusarium oxysporum* f. *batatas* (Wr.) Snyder & Hansen). Steinbauer (203) reported a highly resistant accession from Tinian Island in the Marianas.

SOIL ROT (*Streptomyces ipomoea* (Person & W. J. Martin) Waks. & Henrici). Watson (237) reported results of a variety test in Texas in which B-16, B-4018, L-12 had little or no infection compared with 14.6 per cent in Puerto Rico. The Louisiana Station developed Heartogold variety which has a high degree of resistance.

EGGPLANT

Howard and Desrosiers (100) in Rhode Island reported high resistance to *Phomopsis blight* (*Diaporthe vexans* Gratz) in two collections of Brazilian Gilo and in two Indian varieties, Pegan and Bengal. Decker (64) at the Florida Experiment Station devel-

oped and released for commercial use two highly resistant varieties, Florida Market and Florida Beauty.

Larson (124) found Porto Rican Beauty and selection E-12 from Puerto Rico, both developed for resistance to *Pseudomonas solanacearum* E.F.Sm., to be resistant also to the ring rot bacterium (*Corynebacterium sepedonicum* (Spieck. & Kotth.) Skapt. & Burk.).

PEPPER

BACTERIAL SPOT (*Xanthomonas vesicatoria* (Doidge) Dows.). Horsfall and McDonnell (98) in Connecticut observed the relative resistance of a large collection of strains and varieties of pepper. Among the most resistant were ten strains of Waltham Beauty, two of Yellow Oshkosh, Sunnybrook 833, three strains of Squash, and a few strains of Wonder. In South Carolina Martin (132) observed Santanka and Cayenne to be highly resistant. Burkholder and Li (51) in a study of various isolates from tomato and pepper showed that they differ in their infectivity on pepper varieties, a matter of importance in breeding work.

MOSAICS. The New Jersey Station introduced a variety resistant to tobacco mosaic virus under the name Rutgers World Beater. A more recent introduction is Yolo Wonder developed by Porter and Younkin (163).

In Puerto Rico, Riollano, Adsuar and Rodríguez (181) working on a mosaic disease distinct from that incited by the common tobacco mosaic virus, crossed California Wonder with pungent resistant lines from Puerto Rico and from Mexico. Resistance was controlled by a single dominant gene, and a resistant line of satisfactory commercial value was selected from the cross. McKinney (136) reported a pungent pepper from South Carolina resistant to tobacco-etch virus.

ROOT ROT (*Phytophthora capsici* Leonian). Smith and Minges (201) found Oakview Wonder and a strain of California Wonder to be highly resistant to root rot in California.

IRISH POTATO

NON-PARASITIC DISEASES. Larson and Albert (126, 127) studied susceptibility of potato varieties to internal necrosis of the tuber when grown on sandy soil in central Wisconsin. Among the most

resistant American varieties were Triumph, Red Warba, La Salle and Kasota, while the most susceptible included Ontario, Potomac, Pawnee, Russet Rural and Katahdin. Among British varieties tested, King Edward and Up-to-Date were very resistant, while Arran Consul and Majestic were very susceptible. Massey, Thompson and Smith (133) found that varieties reacted differently in this respect in several locations in New York State. Ontario showed discoloration most consistently in all locations. Folsom (73) studied the reaction of varieties and seedlings to internal mahogany browning which is induced by continuous storage for several months at about 0° C. He pointed out that predisposition to this disease in inherited and that use of very susceptible seedlings in making crosses should be avoided.

RING ROT (*Corynebacterium sepedonicum* (Spieck. & Kotth.) Skapt. & Burk.). Many varieties and seedlings have been tested for resistance by Bonde et al. (44, 45). Two resistant varieties, Teton (177) and Saranac (205), have been introduced.

BROWN ROT (*Pseudomonas solanacearum* E.F.Sm.). Eddins, Ruehle and Townsend (67) reported Katahdin and Chippewa to be moderately resistant in Florida.

WART (*Synchytrium endobioticum* (Schilb.) Perc.). The development of new wart-resistant varieties has continued actively in Europe as illustrated by reports from Great Britain (2), Sweden (209), Norway (131) and Germany (190). New races of the organism were described by Blattný (40) and by Braun (47). Hartman and Akeley (92) and Hartman (91) have shown the following newer American varieties to be resistant: Katahdin, Mohawk, Sequoia, Mesaba, Norkota, Warba, Red Warba, Calrose, Ontario, Pawnee, Kennebec, Chisago.

LATE BLIGHT (*Phytophthora infestans* (Mont.) DBy.). The development of blight-resistant potato varieties has continued with increased vigor in the United States and in European countries (32–39, 186, 214). The progress to date in the United States is summarized by Stevenson et al. (207).

Mills and Peterson (138) have identified three genes for high resistance among progenies of hybrids between *Solanum demissum* and *Solanum tuberosum*. Black (32–39) in Scotland has identified

four *demissum* genes. The following is quoted from his report published in 1952 (38):

"The common strain and six specialized strains of *Phytophthora infestans* have been employed in testing potato varieties and seedling progenies bred from the wild species *S. demissum* for resistance to the disease. Resistance, due to the hypersensitive condition of the protoplasm, is manifested in the presence of major genes, and four such genes have been identified—viz., R_1, R_2, R_3, and R_4. Each gene induces in the plant a hypersensitive response to infection with the common strain and with a particular group of specialized strains of the parasite. The genes are inherited independently in simple Mendelian fashion, but in the segregations three different types of deviations from standard disomic ratios occur due to (*a*) unpaired chromosomes, (*b*) incompatibility factors, and (*c*) partial auto-syndesis. A series of minor genes modify the phenotypic expression of the major gene system and so differentiate grades of hypersensitivity or of susceptibility as the case may be".

"The common strain of *P. infestans* appears to be a population persisting at an equilibrium determined by host range and environmental conditions. Mutations frequently occur, but new forms survive only when host genotypes, to which they are specially adapted, are available".

Müller (141–146) and associates have studied the relation of host and parasite in tubers of susceptible and resistant (hypersensitive) hosts. In both susceptible and resistant varieties the host cell is destroyed after invasion by the parasite, but the process is much slower in the susceptible than in the resistant host. The minimum temperature for fungus invasion of susceptible tubers is just under 5° C.; the optimum, 19–20°; the maximum 25 to 26°. The necrotic reaction of invaded cells sets in at 5 to 11°, and the rate increases with temperature. At 10 to 21° cells of invaded susceptible tubers live six to 14 days, while those of resistant tubers die in one to two days. The necrotic reaction is associated with cell metabolism, and the resistant genotypes are regarded as being capable of reacting so rapidly to the metabolic products of the fungus that the latter is deprived of a suitable substrate upon which to survive. The dying cells go through at least five successive stages, in the last two of which the cytoplasm and walls are infiltrated with what appears to be phenol polymers. When resistant tubers were treated

with solutions of several alcohols at concentrations which did not suppress the germination of sporangia, the length of the necrotic reaction period was lengthened and in some cases thick aerial mycelium bearing sporangia appeared on resistant tubers. The reaction to narcotics was interpreted as one which retarded metabolic activity of the host cell to the extent that the pathogen was able to proceed for a short time in a manner resembling that in the slowly reacting susceptible variety cell. When resistant potato sprouts were used, the necrotic reaction appeared in seven to eight hours at 22°. Different tissues in the same genotype might react at different rates. When distantly related angiosperms, such as cucumber, bean, cabbage and onion, were inoculated, they showed various degrees of sensitivity to the fungus, and within any species different organs might react differently.

Many new varieties have been introduced in the past ten years. Menominee (248), Saranac (205) and Calrose (54) carry the same type of resistance to all races of the pathogen as found in the earlier introduction, Sebago, and in such old varieties as President and Ackersegen. The American varieties Kennebec (10), Essex (174), Pungo (6), Cherokee (6), Empire (172), Placid (173), Virgil (173), Ashworth (173), Chenango (173), Glenmeer (174), Madison (174), Snowdrift (174), Fillmore (174), Cortland (174) and Harford (174) carry one of the *demissum* genes for high resistance. Canadian varieties Keswick (7) and Canso (7), the Scotch varieties Craigs Beauty (3) and Craigs Snow-White (4), and the German varieties Aquila (5), Erica (5), Falke (5), Panther (5), Pommernbote (5) and Urtica (5) each carry one *demissum* gene. The Scotch variety Pentland Ace (9) carries at least two *demissum* genes for high resistance.

SCAB (*Streptomyces scabies* (Thaxt.) Waks. & Henrici). Scab-resistant American varieties introduced in the past ten years include Menominee (248), Ontario (41), Seneca (41), Cayuga (41), Yampa (187) and Cherokee (6). Stevenson et al. in 1939 and 1940 (206) carried out uniform test nurseries in Maine, Colorado, Minnesota and Michigan. The reaction of resistant varieties was quite similar in both years in the four regions. Ellison, Jacob and Cunningham (68) found Ontario and Yampa to be highly resistant in Long Island at a range of soil reaction from pH 4.3 to 7.6.

Hooker and Sass (97), testing plants in sterilized soil in the greenhouse artificially infested with the pathogen, found that susceptible varieties developed stem necrosis, while resistant varieties had little or no such injury. The latter group showed well-developed and continuous periderm with sparse intracellular mycelium, while in susceptible varieties periderm was absent or discontinuous and poorly developed. Vaughan (220) found that wound periderm developed about three times as rapidly in resistant Menominee as in susceptible Rural New Yorker. Krantz and Eide (121, 122) recorded observations on the inheritance of resistance. Johnson and Schaal (113) found a high correlation between the content of chlorogenic acid in outer tuber tissue and resistance in several seedlings.

FUSARIUM WILT (*Fusarium solani* f. *eumartii* (Carpenter) Snyder & Hansen). Extensive trials of varieties and seedlings were conducted by Goss and Jensen (85, 111) in Nebraska. Pontiac, Katahdin, Golden and Sebago were the most resistant. Muncie (147) found Teton to be outstanding in resistance in Michigan.

VERTICILLIUM WILT (*Verticillium albo-atrum* Reinke & Berth.). Wollenweber (259) listed the following varieties as comparatively resistant in Germany: Jubel, Topaz, Bojar, Paulsen's Goldperle, Odenwälder Blaue. McLean (137) in Idaho found best sources of resistance in Katahdin, seedling 41956 and relatives, and in relatives of Jubel and certain other foreign varieties. Populair was the most resistant variety among those tested. In a test of seedlings and varieties in Prince Edward Island, Canada, Ayers (23) found Houma and seedling F4328 highly resistant.

LEAF ROLL. Cockerham (56) reported a high degree of resistance to leaf roll in three varieties, two of which are known to have wild forms in their ancestry. Folsom and Stevenson (74) secured some highly resistant seedlings from Imperia × Earlaine, Kepplestone Kidney × Earlaine, and Houma × Katahdin. Köhler, Bode and Hauschild (120) found Aquila to be highly resistant. McKay and Clinch (135) reported high field resistance in seedlings from Shamrock × Skerry Champion. These results show the possibility of development of highly resistant commercial types through breeding. Webb, Larson and Walker (238, 238*a*) found a wide range

in virulence in 56 isolates from various parts of United States and Canada. They were placed in four groups on the basis of symptoms produced on *Physalis floridana* Rydb. Rozendaal (185) reported three strains of leaf roll—faint, mild, severe—which were shown to be related by cross-protection or premunity tests. The degrees of virulence of the strains appeared to be absolute instead of relative, and they were similar when a large number of potato varieties was tested. Hutton (104) reports using the phloroglucin test for phloem necrosis as a guide for selection of resistant seedlings.

MOSAICS. Cadman (52) concluded that the hypersensitive reaction to virus X is associated with the dominant allele of the gene pair, *Nx nx*. Assuming that potato is an autotetraploid, most necrotic-reacting varieties were interpreted as simplex for the dominant allele. Hutton (105) was of the opinion that the simplex and duplex condition of the gene gave local necrosis, while the triplex gave a severely necrotic reaction. Ladeburg, Larson and Walker (123) found USDA seedling 41956 completely resistant to 18 ringspot isolates of virus X.

The range of resistance in varieties and seedlings of potato and in species of *Solanum* to virus Y has been reported by Schultz, Stevenson and Akeley (193) in the United States, Bawden and Kassanis (30, 31) in England, Cockerham (56–59) in Scotland, Hutton (103, 106) in Australia, Stelzner (204) and Ross and Baerecke (184) in Germany. A wide range of reactions exists, but as yet no line comparable to USDA seedling 41956 in relation to virus X has been found in *Solanum tuberosum*. However, Ross (183) claims immunity from virus Y in *Solanum antipovicjii, S. ajuscoense* and several other members of the series *longipedicellata*. Darby, Larson and Walker (61) studied 25 isolates on 22 standard varieties. The relative virulence of most of the 18 isolates was much the same for the 22 varieties, but there were several outstanding exceptions. Isolate 7, severe on most varieties, produced only mild primary symptoms on Snow Drift, whereas isolate 18, mild on most varieties, was moderately severe on Snow Drift. This is somewhat at variance with the results of Bawden and Kassanis (30) who, working with four varieties and seven isolates, found that the same order virulence between isolates held for all varieties tested.

YELLOW DWARF. Rieman and McFarlane (179) noted in 19 plots exposed to natural infection that Sebago averaged 0.5 per cent infected plants, while Russet Rural averaged 18 per cent. Since infected plants of Sebago were as severely diseased as those of Russet Rural, they suggested that the low incidence of the disease in Sebago was due to avoidance of that variety by the insect vector. Larson (125) found Russet Burbank, Red Warba and Sebago to show a high degree of field resistance. He found the vector as numerous on resistant as on susceptible varieties and concluded that field resistance was due to some factor effective at the threshold of infection. He also noted that tubers of infected plants of the resistant varieties did not show the malformation and internal necrosis characteristic of those from infected plants of susceptible varieties.

TOMATO

BACTERIAL DISEASES. Roque (182) in Puerto Rico developed a variety resistant to wilt (*Pseudomonas solanacearum* E.F.Sm.) from a cross between Louisiana Pink and a native resistant type. This variety was also highly resistant in North Carolina (1). Alexander et al. (13) recorded observations on the reaction of various species of *Lycopersicon* to bacterial canker (*Corynebacterium michiganense* (E.F.Sm.) Jensen) and bacterial spot (*Xanthomonas vesicatoria* (Doidge) Dows.).

LATE BLIGHT (*Phytophthora infestans* (Mont.) DBy.). Although Andrus (17) found a number of varieties comparatively resistant during a field epidemic in South Carolina, these results have not been confirmed elsewhere. Walter and Conover (234) found two small-fruited collections in Florida to be resistant there, but resistance did not hold when they were tested in North Carolina and West Virginia. Progress in selection for resistance was reported in Maine by Bonde and Murphy (43) and in Canada by Ferguson, Lyall and Racicot (71). Gallegly (78) described three distinct physiologic races on tomato. All strains tested were susceptible to at least one race.

VERTICILLIUM WILT (*Verticillium albo-atrum* Reinke & Berth.). Essar (195), Riverside (196) and Simi (128) are resistant varieties developed in California. The last two are also resistant to Fusarium wilt. Schroeder (191) found highly significant differ-

ences between varieties at Geneva, New York. Improved Wasatch Beauty, Gem, John Baer and Early Jersey were among the most susceptible, while Stokesdale, Longred and Wisconsin 55 were the least affected. In 1951 Schaible, Cannon and Waddoups (188) reported a single dominant gene which controlled high resistance in a line, W6, secured from a cross between Peru Wild and Century. This source of resistance offers unusual promise for the incorporation of *Verticillium* resistance into commercial varieties.

LEAF MOLD (*Cladosporium fulvum* Cke.). The resistant varieties Globelle and Vetomold, introduced in the late 30's, soon succumbed to a new race of the pathogen, as shown by Alexander (11) in 1942. The problem of variability of the pathogenicity of the fungus has been studied extensively by Bailey (24). He reported nine races which were distinguished on the basis of host reaction, the latter being divided into three categories, i.e., immune, resistant and susceptible. Potentate was susceptible to all seven races. Vetomold was immune from races 1 and 2 but susceptible to races 5, 6, 7, 8 and 9. V-121 was resistant to 1, 2, 5 and 8, susceptible to 6, 7 and 9. Sterling Castle was resistant to 1, 5, 7 and 9 but susceptible to 2, 6 and 8. V-473 was immune from 1, 2 and 9, resistant to 5 and 7, and susceptible to 6 and 8. Vineland strain 160 of Red Currant (*Lycopersicon pimpinellifolium*) was immune from 1 and 5, and resistant to 6, 7, 8 and 9. H-112215M and *L. hirsutum* were immune from 1, 5, 6, 7, 8 and 9. *L. hirsutum* var. *glabratum* was immune from 1, 3, 8 and 9 and resistant to 6 and 7. The reactions of the last four plant lines to race 2 were not reported.

GRAY LEAF SPOT (*Stemphylium solani* G. F. Weber). Andrus and Reynard (18) reported high resistance in *L. pimpinellifolium* and in hybrids between the latter and *L. esculentum*. Hendrix and Frazier (95) in Hawaii found resistance in Red Currant and Targinnie Red to be governed by a single dominant gene. Frazier et al. (75) introduced seven new varieties in 1950 which had combined resistance to spotted wilt, Fusarium wilt and gray leaf spot.

EARLY BLIGHT (*Alternaria solani* (Ell. & Martin) L. R. Jones & Grout). Andrus et al. (20) and Moore and Reynard (140) reported a number of varieties which were highly resistant to the collar-rot phase of early blight. Reynard and Andrus (175) studied inheritance of the resistant character in Devon Surprise and found

it to be controlled by a single gene pair in which susceptibility was partially dominant over resistance. Southland is a new variety which is resistant to Fusarium wilt and collar rot. No satisfactory resistance to the leaf blight and fruit rot stages of early blight has been found in tomato. Resistance in other species of *Lycopersicon* has been reported by Locke (130) and by Alexander et al. (13).

FUSARIUM WILT (*Fusarium oxysporum* f. *lycopersici* (Sacc.) Snyder & Hansen). Wellman (243, 244, 245) studied variability of the common race of the pathogen. In Ohio and Missouri Alexander and Tucker (14) found a second race of the wilt fungus which was highly pathogenic on plants carrying single-gene resistance to race 1. The new race is so far very restricted in known distribution. Gerdeman and Finley (80) considered that there was probably a one-step transition between the two races. Porte and Wellman (162) reported on methods for the improvement of tomato for wilt resistance by crossing with *L. pimpinellifolium*. The first commercial variety introduced which carried single-gene resistance was Pan America, introduced by Porte and Walker (160) in 1941. Alexander (12) introduced Ohio W-R Globe, a greenhouse forcing variety in 1949. Other varieties with single-gene resistance now available include Southland, Sunray (161), Jefferson, Golden Sphere (8) and several from Hawaii (75). Riverside (196) and Simi (128) are varieties which are resistant to both Fusarium wilt and Verticillium wilt.

Heinze and Andrus (94) studied Fusarium wilt development in grafts made in various ways between resistant Pan America and susceptible Bonny Best. Since Pan America scions wilted severely when supported by Bonny Best roots, they concluded that the resistant principle was located in the root system. Snyder, Baker and Hansen (202) studied the same two varieties. They found that when inoculation was made through incised tap roots, the xylem in both became infected up through the aerial stem, although the number of vessels infected in Pan America was considerably less than in Bonny Best. They were inclined to believe that resistance was a function of the living cells of the host and was exerted in the young roots at the time of penetration to prevent invasion of the lumina of the xylem tubes. Brock (49) found that, although roots of Pan America were invaded by the pathogen and vascular browning occurred in the subterranean xylem, plants remained

resistant in the field. Scheffer and Walker (189) approached this question with a still different technique. They immersed cut ends of stems of susceptible and single-gene resistant plants in a suspension of microconidia under conditions favoring a high rate of transpiration. After several hours when spores had been carried widely throughout the plant in the transpiration stream, the cuttings were rooted and planted under conditions favorable for wilt. In ten to 15 days the disease appeared in both varieties, and the fungus could be isolated readily from petioles but not from roots. Resistant varieties soon recovered and grew normally, while in susceptible plants the disease became progressively more severe. They interpreted this as evidence that the resistant character is not localized in the roots but is present and functional throughout the plants. Walker and Foster (224) showed that single-gene resistance was very stable at different host nutrient levels.

ANTHRACNOSE (*Colletotrichum phomoides* (Sacc.) Chester). Wilson (255) and Wilson and Runnels (257) observed the incidence of this disease on a large number of varieties in Ohio. They found that determinate varieties as a group were more severely affected than indeterminate varieties as a group. Likewise pink-fruited varieties were for the most part more severely affected than red-fruited varieties. Schroeder (191) found two varieties, T-16 and Club 86, of 17 tested at Geneva, New York, to have markedly low incidence of anthracnose.

SEPTORIA LEAF SPOT (*Septoria lycopersici* Speg.). Andrus and Reynard (19) found 12 out of 267 accessions of *Lycopersicon hirsutum* or *L. peruvianum* descent, or related to some other primitive type, to have small, dark, reddish-brown lesions with few or no pycnidia developing after penetration. This character was inherited as a single dominant factor. In using this character in a backcross breeding program, Lincoln and Cummins (129) found in the sixth backcross no plants with resistance equal to that of the resistant parent. Modifying genes may have supressed expression of resistance. Locke (130) noted one strain of *L. hirsutum* which was highly resistant to Septoria leaf spot.

SPOTTED WILT. Holmes (96) in New Jersey reported a type of resistance in Argentinian varieties Rey de los Tempranos and Mangana which was controlled by a single recessive gene. Smith

and Gardner (200) reported a high level of resistance in Red Currant tomato (*L. pimpinellifolium*) in the field. It was susceptible, however, when inoculated experimentally. German Sugar was moderately resistant in the field. When Red Currant and German Sugar were crossed with susceptible varieties, an intermediate level of resistance prevailed in the F_1 and the level of resistance of the resistant parent was not recovered in succeeding generations. Kikuta, Hendrix and Frazier (118) developed Pearl Harbor, a moderately resistant variety in Hawaii, from a Red Currant hybrid from Smith and Gardner crossed with Bonny Best. Frazier et al. (75) later developed seven new varieties in Hawaii equal to Pearl Harbor in spotted wilt resistance and also resistant to Fusarium wilt and to gray leaf spot. Hutton and Peak (107) in Australia found Pearl Harbor and Mangana very susceptible. Starting with another highly resistant strain of Red Currant, they found resistance highly recessive and multigenic. In backcrosses with Sioux subjected to rigid screening for resistance in the greenhouse, they stabilized resistance in the fourth generation.

BIBLIOGRAPHY

1. Anon. 1943. N. C. Agr. Exp. Sta., Ann. Rep. **1942–43**.
2. ————. 1944–48. Trials of potatoes for immunity from wart disease. Jour. Min. Agr. [Gt. Brit.] **51**: 382–383; **52**: 475–476; **54**: 574–575.
3. ————. 1947. Scot. Soc. Res. Plant Breed. Ann. Rep. **1947**: 15.
4. ————. 1948. *Ibid.* **1948**: 17.
5. ————. 1950. Nya tiska potatissorter. Tidsskr. Lantm. **32**: 84.
6. ————. 1951. New varieties released. Am. Potato Jour. **28**: 641–642.
7. ————. 1951. New potato varieties released. *Ibid.* **28**: 697–699.
8. ————. 1951. Golden Sphere tomato. Seed World **68**(9) : 10.
9. ————. 1952. Scot. Plant Breed. Sta., Ann. Rep. **1952**: 33.
10. Akeley, R. V., F. J. Stevenson and E. S. Schultz. 1948. Kennebec: a new potato variety resistant to late blight, mild mosaic, and net necrosis. Am. Potato Jour. **25**: 351–361.
11. Alexander, L. J. 1942. A new strain of the tomato leaf-mold fungus (*Cladosporium fulvum*). Phytopath. **32**: 901–904.
12. ————. 1949. Ohio W-R Globe, a new wilt-resistant glasshouse tomato variety. Ohio Agr. Exp. Sta., Res. Bul. 689.
13. ————, R. E. Lincoln and V. Wright. 1942. A survey of the genus *Lycopersicon* for resistance to the important tomato diseases occurring in Ohio and Indiana. Plant Dis. Rep., Suppl. **136**: 52–85.
14. ———— and C. M. Tucker. 1945. Physiological specialization in the tomato wilt fungus *Fusarium oxysporum* f. *lycopersici*. Jour. Agr. Res. **70**: 303–313.
15. Ali, M. A. 1950. Genetics of resistance to the common bean mosaic (bean virus 1) in the bean (*Phaseolus vulgaris* L.). Phytopath. **40**: 69–79.

16. ANDERSON, M. E. 1941. Sensation Refugees, two new mosaic-resistant varieties. Canner **92**(7): 14–15.
17. ANDRUS, C. F. 1946. Resistance of tomato varieties to late blight in South Carolina. Plant Dis. Rep. **30**: 269–270.
18. ———— and G. B. REYNARD. 1942. Relative resistance of tomato varieties, selections, and crosses to defoliation by *Alternaria* and *Stemphylium*. U. S. Dept. Agr., Cir. 652.
19. ———— and ————. 1945. Resistance to *Septoria* leaf spot and its inheritance in tomatoes. Phytopath. **35**: 16–24.
20. ————, ————, H. JORGENSEN and J. EADES. 1942. Collar rot resistance in tomatoes. Jour. Agr. Res. **65**: 339–346.
21. ———— and B. L. WADE. 1942. The factorial interpretation of anthracnose resistance in beans. U. S. Dept. Agr., Tech. Bul. 810.
22. ARMSTRONG, G. M., and J. K. ARMSTRONG. 1952. Physiologic races of the fusaria causing wilts of the Cruciferae. Phytopath. **42**: 255–257.
23. AYERS, G. W. 1952. Studies on *Verticillium* wilt. Am. Potato Jour. **29**: 201–205.
24. BAILEY, D. L. 1950. Studies in racial trends and constancy in *Cladosporium fulvum* Cooke. Canad. Jour. Res. C. **28**: 535–565.
25. BAIN, D. C. 1952. Reaction of *Brassica* seedlings to blackrot. Phytopath. **42**: 497–500.
26. BARNES, W. C. 1948. The performance of Palmetto, a new downy mildew-resistant cucumber variety. Proc. Am. Soc. Hort. Sci. **51**: 437–441.
27. ————. 1950. Santee's quite a cucumber. Southern Seedsman **13**(1): 1, 16.
28. ————. 1951. Mosaic resistant Parris Island new cos lettuce may restore lost industry in 1952. *Ibid.* **14**(12): 24, 80.
29. ———— and W. M. EPPS. 1950. Some factors related to the expression of resistance of cucumbers to downy mildew. Proc. Am. Soc. Hort. Sci. **56**: 377–380.
30. BAWDEN, F. C., and B. KASSANIS. 1946. Varietal differences in susceptibility to potato virus Y. Ann. Appl. Biol. **33**: 46–50.
31. ———— and ————. 1947. The behavior of some naturally occurring strains of potato virus Y. *Ibid.* **34**: 503–516.
32. BLACK, W. 1943. Inheritance of resistance to two strains of blight. (*Phytophthora infestans* de Bary) in potatoes. Trans. Roy. Soc. Edinb. **61**: 137–147.
33. ————. 1945. Inheritance of resistance to blight (*Phytophthora infestans*) in potatoes: unbalanced segregations. Proc. Roy. Soc. Edinb. B. **62**, Part II: 171–181.
34. ————. 1947. Blight resistance in potatoes. Jour. Min. Agr. [Gt. Brit.] **54**: 198–200.
35. ————. 1947. Blight in relation to potato breeding. Ann. Appl. Biol. **34**: 631–633.
36. ————. 1949. Inheritance of resistance to blight ('*Phytophthora infestans*') in potatoes: comparison of A and B strains. Proc. Roy. Soc. Edinb. B. **63**, Part III: 290–301.
37. ————. 1950. Inheritance of resistance to blight (*Phytophthora infestans*) in potatoes: Strain C and its relationship. *Ibid.* B. **64**: Part II: 216–228.
38. ————. 1952. Inheritance of resistance to blight (*Phytophthora infestans*) in potatoes: inter-relationships of genes and strains. *Ibid.* B. **64**: 312–352.
39. ———— and J. G. HAIGH. 1947. Strains of potato blight in Scotland. Scot. Jour. Agr. **27**: 49–50.

40. BLATTNÝ, C. 1942. Vorläufige Mitteilung über die Rassen des Kartoffelkrebses *Synchytrium endobioticum* (Schilb.) Perc. Ann. Akad. Tchéchoslov. Agr. **17**: 40–46.
41. BLODGETT, F. M., and F. J. STEVENSON. 1946. The new scab-resistant potatoes, Ontario, Seneca, and Cayuga. Am. Potato Jour. **23**: 315–329.
42. BOHN, G. W., and T. W. WHITAKER. 1951. Recently introduced varieties of head lettuce and methods used in their development. U. S. Dept. Agr., Cir. 881.
43. BONDE, R., and E. F. MURPHY. 1952. Resistance of certain tomato varieties and crosses to late blight. Maine Agr. Exp. Sta., Bul. 497.
44. ———, F. J. STEVENSON and R. V. AKELEY. 1947. Breeding potatoes for resistance to ring rot. Phytopath. **37**: 539–555.
45. ———, ———, C. F. CLARK and R. V. AKELEY. 1942. Resistance of certain potato varieties and seedling progenies to ring rot. *Ibid.* **32**: 813–819.
46. BRAUN, A. E. 1942. Resistance of watermelon to the wilt disease. Am. Jour. Bot. **29**: 683–684.
47. BRAUN, H. 1942. Biologische Spezialisierung bei *Synchytrium endobioticum* (Schilb.) Perc. Zeits. Pflanzenkrank. **52**: 481–486.
48. BRIERLEY, P., and F. F. Smith. 1946. Reaction of onion varieties to yellow-dwarf virus and to three similar viruses from shallot, garlic, and narcissus. Phytopath. **36**: 292–296.
49. BROCK, R. D. 1948. The nature of *Fusarium* wilt resistance in the tomato variety Pan America. Jour. Austral. Inst. Agr. Sci. **14**: 78–80.
50. BURKHOLDER, W. H., and E. T. BULLARD. 1946. Varietal susceptibility of beans to *Xanthomonas phaseoli* var. *fuscans*. Plant Dis. Rep. **30**: 446–448.
51. ——— and C. C. LI. 1941. Variations in *Phytomonas vesicatoria*. Phytopath. **31**: 753–755.
52. CADMAN, C. H. 1942. Autotetraploid inheritance in the potato: some new evidence. Jour. Genet. **44**: 33–52.
53. CASS SMITH, W. P., H. L. HARVEY and O. M. Goss. 1951. "Westralia". A new rust resistant pole bean. Jour. Agr. West Australia **28**: 317–324.
54. CLARK, C. F. 1946. The Calrose potato: a new variety possessing resistance to late blight. Am. Potato Jour. **23**: 343–347.
55. CLARKE, A. E., H. A. JONES and T. M. LITTLE. 1944. Inheritance of bulb color in the onion. Genetics **29**: 569–575.
56. COCKERHAM, G. 1943. Potato breeding for virus resistance. Ann. Appl. Biol. **30**: 105–108.
57. ———. 1943. The reactions of potato varieties to viruses X, A, B, and C. *Ibid.* **30**: 338–344.
58. ———. 1945. Some genetical aspects of resistance to plant viruses. *Ibid.* **32**: 280–281.
59. ———. 1952. Breeding for resistance to potato viruses. Proc. Conf. Potato Virus Dis., Wageningen-Lisse, **1951**: 37–39.
60. COOK, H. T., T. J. NUGENT, G. K. PARRIS and R. P. PORTER. 1947. *Fusarium* wilt of spinach and development of a resistant variety. Va. Truck Exp. Sta., Bul. 110.
61. DARBY, J. F., R. H. LARSON and J. C. WALKER. 1951. Variation in virulence and properties of potato virus Y strains. Wis. Agr. Exp. Sta., Res. Bul. 177.
62. DAVIS, G. N. 1952. Baby Klondike watermelon. Calif. Agr. **6**(5): 15.
63. DEAN, L. L., and C. W. HUNGERFORD. 1946. A new bean mosaic in Idaho. Phytopath. **36**: 324–326.
64. DECKER, P. 1951. *Phomopsis*-blight resistant eggplants. *Ibid.* **41**: 9.

65. DUNDAS, B. 1941. Further studies on the inheritance of resistance to powdery mildew of beans. Hilgardia **13**: 551–565.
66. ————. 1942. Breeding beans for resistance to powdery mildew and rust. Phytopath. **32**: 828.
67. EDDINS, A. H., G. D. RUEHLE and G. R. TOWNSEND. 1946. Potato diseases in Florida. Fla. Agr. Exp. Sta., Bul. 427.
68. ELLISON, J. H., W. C. JACOB and H. S. CUNNINGHAM. 1951. Effect of soil reaction on the performance of certain scab-resistant and susceptible potato varieties. Am. Potato Jour. **28**: 721–727.
69. EPPS, W. M. 1947. A new wilt-resistant watermelon. Phytopath. **37**: 433.
70. ———— and C. D. SHERBAKOFF. 1949. Wilt detours Miles melons. Southern Seedsman **12**(4) : 13.
71. FERGUSON, W. L., L. H. LYALL and H. N. RACICOT. 1952. Tomato breeding for resistance to *Phytophthora infestans* (Mont.) de By. 1. Method of inoculation and preliminary results. Sci. Agr. **32**: 57–66.
72. FISHER, H. H. 1952. New physiologic races of bean rust (*Uromyces phaseoli typica*). Plant Dis. Rep. **36**: 103–105.
73. FOLSOM, D. 1947. Inheritance of predisposition of potato varieties to internal mahogany browning of the tubers. Am. Potato Jour. **24**: 294–298.
74. ———— and F. J. STEVENSON. 1946. Resistance of potato seedling varieties to the natural spread of leaf roll. *Ibid.* **23**: 247–264.
75. FRAZIER, W. A., R. K. DENNETT, J. W. HENDRIX, C. F. POOLE and J. C. GILBERT. 1590. Seven new tomatoes. Varieties resistant to spotted wilt, *Fusarium* wilt, and gray leaf spot. Hawaii Agr. Exp. Sta., Bul. 103.
76. ———— and J. W. HENDRIX. 1949. Hawaiian Wonder. New rust-resistant pole green bean. Hawaii Agr. Exp. Sta., Cir. 28.
77. FULTON, J. P. 1950. Studies on strains of cucumber virus 1 from spinach. Phytopath. **40**: 729–736.
78. GALLEGLY, M. E. 1952. Physiologic races of the tomato late blight fungus. *Ibid.* **42**: 461–462.
78*a*. GANTE, T. 1951. Hernieresistenz bei Weisskohl. Zeits. Pflanzenzücht. **30**: 188–197.
79. GASIORKIEWICZ, E. C., R. H. LARSON, J. C. WALKER and M. A. STAHMANN. 1952. Induced variability in *Pyrenochaeta terrestris* by nitrogen mustard. *Ibid.* **42**: 183–192.
80. GERDEMAN, J. W., and A. M. FINLEY. 1951. The pathogenicity of races 1 and 2 of *Fusarium oxysporum* f. *lycopersici*. *Ibid.* **41**: 238–244.
81. GERRITSEN, J. D., and H. BURGMANS. 1940. *Ascochyta*-ziekten bij erwten. Tijdschr. over Plantenziekten **46**: 57–82.
82. GILPATRICK, J. D., and L. V. BUSCH. 1950. Studies on the pathogenicity of different isolates of *Ascochyta pisi* Lib. Plant Dis. Rep. **34**: 383–387.
83. GODFREY, G. H. 1951. Rio Sweet. Southern Seedsman **14**(3) : 65, 74.
84. GORENZ, A. M., R. H. LARSON and J. C. WALKER. 1949. Factors affecting pathogenicity of pink root fungus in onions. Jour. Agr. Res. **78**: 1–18.
85. GOSS, R. W., and J. H. JENSEN. 1941. Varietal susceptibility of potatoes to *Fusarium* wilt. Am. Potato Jour. **18**: 209–212.
86. GROGAN, R. G., and J. C. WALKER. 1948. The relation of common mosaic to black root of bean. Jour. Agr. Res. **77**: 315–331.
87. HARE, W. W., J. C. WALKER and E. J. DELWICHE. 1949. Inheritance of a gene for near-wilt resistance in the garden pea. *Ibid.* **78**: 239–250.

88. HARLAND, S. C. 1948. Inheritance in immunity to mildew in Peruvian forms of *Pisum sativum*. Heredity **2**: 263–269.
89. HARRISON, A. L. 1936. Varietal susceptibility of lima bean to mosaic. Plant Dis. Rep. **20**: 291.
90. HARTER, L. L., and W. J. ZAUMEYER. 1941. Differentiation of physiologic races of *Uromyces phaseoli typica* on bean. Jour. Agr. Res. **62**: 717–731.
91. HARTMAN, R. E. 1951. Potato wart in America. Plant Dis. Rep. **35**: 268–271.
92. ———— and R. V. AKELEY. 1944. Potato wart in America. Am. Potato Jour. **21**: 283–288.
93. HATFIELD, W. C., J. C. WALKER and J. H. OWEN. 1948. Antibiotic substances in onion in relation to disease resistance. Jour. Agr. Res. **77**: 115–135.
94. HEINZE, P. H., and C. F. ANDRUS. 1945. Apparent localization of *Fusarium* wilt resistance in the Pan America tomato. Am. Jour. Bot. **32**: 62–66.
95. HENDRIX, J. W., and W. A. FRAZIER. 1949. Studies on the inheritance of *Stemphylium* resistance in tomatoes. Hawaii Agr. Exp. Sta., Tech. Bul. 8.
96. HOLMES, F. O. 1948. Resistance to spotted wilt in tomato. Phytopath. **38**: 467–473.
97. HOOKER, W. J., and J. E. SASS. 1948. Some histological features of potato stem necrosis associated with *Actinomyces scabies*. *Ibid.* **38**: 14.
98. HORSFALL, J. G., and A. D. MCDONNELL. 1940. Varietal susceptibility of peppers to bacterial spot. Plant Dis. Rep. **24**: 34–36.
99. HOUGAS, R. W., G. H. RIEMAN and G. W. STOKES. 1952. Resistance to white rust in horseradish seedlings. Phytopath. **42**: 109–110.
100. HOWARD, F. L., and R. DESROSIERS. 1941. Studies on the resistance of eggplant varieties to *Phomopsis* blight. Proc. Am. Soc. Hort. Sci. **39**: 337–340.
101. HUNGERFORD, C. W. 1952. Disease resistant field beans for Idaho. Idaho Agr. Exp. Sta., Cir. 118.
102. HUNTER, A. W. S., and F. H. WHITE. 1950. Breeding for disease-resistance in Canada. Empire Jour. Exp. Agr. **18**: 220.
103. HUTTON, E. M. 1946. The relationship between necrosis and resistance to virus Y in the potato. 3. Interrelation with virus C. Jour. Austral. Counc. Sci. & Ind. Res. **19**: 273–282.
104. ————. 1949. The significance of the necrotic phloem reaction in the potato to the leaf-roll virus. Austral. Jour. Sci. Res. B. **3**: 249–270.
105. ————. 1951. Possible genotypes conditioning virus resistance in the potato and tomato. Jour. Austral. Inst. Agr. Sci. **17**: 132–138.
106. ————, and J. G. BALD. 1945. The relationship between necrosis and resistance to virus Y in the potato. 1. Greenhouse results. Jour. Austral. Counc. Sci. & Ind. Res. **18**: 48–52.
107. ———— and A. R. PEAK. 1949. Spotted wilt resistance in the tomato. Jour. Austral. Inst. Agr. Sci. **15**: 32–36.
108. IVANOFF, S. S. 1944. Resistance of cantaloupes to downy mildew and the melon aphid. Jour. Hered. **35**: 34–39.
109. JENKINS, J. M., JR. 1942. Downy mildew resistance in cucumbers. *Ibid.* **33**: 34–38.
110. ————. 1946. Studies on the inheritance of downy mildew resistance and of other characters in cucumber. *Ibid.* **37**: 267–271.
111. JENSEN, J. H., and R. W. GOSS. 1941. Infection of first-year potato seedlings with *Fusarum solani* var. *eumartii*. Am. Potato Jour. **18**: 239–242.

112. ———— and R. W. Goss. 1942. Physiological resistance to halo blight in beans. Phytopath. **32:** 246–253.
113. Johnson, G., and L. A. Schaal. 1952. Relation of chlorogenic acid to scab resistance in potatoes. Science **115:** 627–629.
114. Jones, H. A. 1946. Problems and progress in onion breeding. Herbertia **11:** 275–294.
115. ———— and A. E. Clarke. 1942. A natural amphidiploid from an onion species hybrid. Jour. Hered. **33:** 25–32.
116. ————, D. R. Porter and L. D. Leach. 1937. Breeding for resistance to downy mildew. Hilgardia **12:** 531–550.
117. ————, J. C. Walker, T. M. Little and R. H. Larson. 1946. Relation of color-inhibiting factor to smudge resistance in onion. Jour. Agr. Res. **72:** 259–264.
118. Kikuta, K., Hendrix, J. W. and W. A. Frazier. 1945. Pearl Harbor, a tomato resistant to spotted wilt in Hawaii. Hawaii Agr. Exp. Sta., Cir. 24.
119. Klimke, A. 1941. Untersuchungen über die *Corynespora*-Krankheit der Gurken und die Resistenz deutscher Gurkensorten. Phytopath. Zeits. **13:** 401–435.
120. Köhler, E., O. Bode and J. Hauschild. 1949. Vergleichende Untersuchungen über die Blattroll-Resistenz von 5 mittelspäter Kartoffelsorten. Nachrbl. Biol. Zent.-Anst. **1:** 81–82.
121. Krantz, F. A., and C. J. Eide. 1941. Inheritance of reaction to common scab in the potato. Jour. Agr. Res. **63:** 219–231.
122. ———— and ————. 1948. Resistance to common scab of potatoes in parental clones and in their hybrid progenies. Am. Potato Jour. **25:** 294–300.
123. Ladeburg, R. C., R. H. Larson and J. C. Walker. 1950. Origin, interrelation, and properties of ringspot strains of virus X in American potato varieties. Wis. Agr. Exp. Sta., Res. Bul. 165.
124. Larson, R. H. 1944. The ring rot bacterium in relation to tomato and eggplant. Jour. Agr. Res. **69:** 309–325.
125. ————. 1945. Resistance in potato varieties to yellow dwarf. *Ibid.* **71:** 441–451.
126. ———— and A. R. Albert. 1945. Physiological internal necrosis of potato tubers in Wisconsin. *Ibid.* **71:** 487–505.
127. ———— and ————. 1949. Relation of potato varieties to incidence of physiological internal tuber necrosis. Am. Potato Jour. **26:** 427–431.
128. Lesley, J. W., J. T. Middleton and C. D. McCarty. 1952. Simi, a processing tomato resistant to *Verticillium* and *Fusarium* wilts. Hilgardia **21:** 289–299.
129. Lincoln, R. E., and G. B. Cummins. 1949. *Septoria* blight resistance in the tomato. Phytopath. **39:** 647–655.
130. Locke, S. B. 1949. Resistance to early blight and *Septoria* leaf spot in the genus *Lycopersicon*. *Ibid.* **39:** 829–836.
131. Lunden, A. P. 1950. Undersøkelser over reaksjon mot kreft (*Synchytrium endobioticum*) has potet. Meld. Norg. Landbrkøgsk. **30:** 1–48.
132. Martin, J. A. 1948. Bacterial spot resistance in peppers. Proc. Am. Soc. Hort. Sci. **52:** 336–340.
133. Massey, P. H., Jr., H. C. Thompson, and O. Smith. 1952. Varietal susceptibility of potatoes to internal black spot. Am. Potato Jour. **29:** 127–135.
134. Mastenbroek, C. 1943. De vatbaarheid van boonenrassen voor de vetvlekkenziekte. Tidschr. over Plantenziek. **49:** 135–162.
135. McKay, R., and P. E. M. Clinch. 1951. Observations on the inheritance of field resistance to leaf roll of potatoes. (Shamrock × Skerry Champion). Sci. Proc. Roy. Dublin Soc. n.s. **25:** 225–233.

136. McKinney, H. H. 1952. Two strains of tobacco-mosaic virus, one of which is seed-borne in an etch-immune pungent pepper. Plant Dis. Rep. **36**: 184–187.
137. McLean, J. G. 1952. Results of testing lines and varieties of potatoes for field resistance to *Verticillium* wilt. Phytopath. **42**: 26.
138. Mills, W. R., and L. C. Peterson. 1952. The development of races of *Phytophthora infestans* (Mont.) de Bary on potato hybrids. Phytopath. **42**: 26.
139. Moore, W. C. 1949. The significance of plant diseases in Great Britain. Ann. Appl. Biol. **36**: 295–306.
140. Moore, W. D., and G. B. Reynard. 1945. Varietal resistance of tomato seedlings to the stem-lesion phase of *Alternaria solani*. Phytopath. **35**: 933–935.
141. Müller, K. O. 1950. Affinity and reactivity of angiosperms to *Phytophthora infestans*. Nature **166**: 392–395.
142. ————. 1951. Ueber die Herkunft der W-Sorten, ihre Entwicklungsgeschichte und ihre bisherige Nutzung in der praktischen Kartoffelzüchtung. Zeits. Pflanzenzücht. **29**: 366–387.
143. ———— and L. Behr. 1949. 'Mechanism' of *Phytophthora*-resistance of potatoes. Nature **163**: 498–499.
144. ———— and H. Börger. 1941. Experimentelle Untersuchungen über die Phytophthora-Resistenz der Kartoffel. Zugleich ein Beitrag zum Problem der "erworbenen-Resistenz" im Pflanzenreich. Arb. Biol. Anst. Land Forstw. **23**: 189–231.
145. ———— and Griesinger, R. 1942. Der Einfluss der Temperatur auf die Reaktion von anfälligen und resistenten Kartoffelsorten gegenüber *Phytophthora infestans*. Ang. Bot. **24**: 130–149.
146. ————, G. Meyer and M. Klinkowski. 1939. Physiologische-genetische Untersuchungen über die Resistenz der Kartoffel gegen *Phytophthora infestans*. Naturwiss. **27**: 765–768.
147. Muncie, J. H. 1949. Reaction of potato varieties to infection by *Fusarium eumartii* Carpenter. Mich. Agr. Exp. Sta., Quart. Bul. **31**: 270–274.
148. Munger, H. M. 1944. Iroquois muskmelon is resistant to *Fusarium* wilt. Farm Res. (N. Y. State Sta.) **10**(2): 20.
149. ————. 1950. Two new mosaic-resistant cucumbers. *Ibid.* **16**(4): 13.
150. ———— and A. G. Newhall. 1952. Emerson Pascal. A blight-resistant celery. *Ibid.* **18**(1): 11.
151. Murphy, D. M. 1940. Bean improvement and bean diseases in Idaho. Idaho Agr. Exp. Sta., Bul. 238.
152. Nelson, R. 1951. Michigan State Green-Gold: a new celery resistant to *Fusarium* yellows. Mich. Agr. Exp. Sta., Quart. Bul. **33**: 280–285.
153. Noll, W. 1940. Ueber weitere Befallsymtome und Massnahm zur Verhütung von Schäden durch *Ascochyta pinodella* Jones, *A. pisi* Lib. und *Mycosphaerella pinodes* (Berk. u. Blox.) Stone bei Erbsen. Zeits. Pflanzenkrank. **50**: 49–71.
154. Owen, J. H., J. C. Walker and M. A. Stahmann. 1950. Pungency, color, and moisture supply in relation to disease resistance in the onion. Phytopath. **40**: 292–297.
155. Parris, G. K. 1948. Further observations on the inheritance of resistance of *Fusarium* wilt in watermelon. Plant Dis. Rep. **32**: 378–379.
156. ————. 1951. Downy mildew resistant strains of watermelon from the Dominican Republic, West Indies. *Ibid.* **35**: 399–401.
157. ————. 1952. Diseases of watermelons. Fla. Agr. Exp. Sta., Bul. 496.

158. PIERCE, W. H. 1948. Resistance to powdery mildew in peas. Phytopath. **38:** 21.
159. POPE, D. T., H. M. MUNGER and J. CAREW. 1952. Chlorosis in celery—an inherited magnesium deficiency. Farm Res. (N. Y. State Sta.) **18**(2) : 10.
160. PORTE, W. S., and H. B. WALKER. 1941. The Pan America tomato, a new red variety highly resistant to *Fusarium* wilt. U. S. Dept. Agr., Cir. 611.
161. ———— and H. B. WALKER. 1950. Two members of the Beltsville Station relate the interesting facts about Sunray, a new golden wilt resistant tomato. Seed World **66**(4) : 10, 12.
162. ———— and F. L. WELLMAN. 1941. Development of interspecific tomato hybrids of horticultural value and highly resistant to *Fusarium* wilt. U. S. Dept. Agr., Cir. 584.
163. PORTER, D. R., and S. G. YOUNKIN. 1952. Yolo Wonder pepper. Seed World **70**(3) : 8, 50.
164. POUND, G. S. 1947. Reactions of cabbage varieties to mosaic viruses. Jour. Agr. Res. **75:** 19–30.
165. ————. 1952. Relation of air temperature and virus concentration to mosaic resistance in cabbage. Phytopath. **42:** 83–88.
166. ———— and P-C. CHEO. 1952. Studies on resistance to cucumber virus 1 in spinach. *Ibid.* **42:** 301–306.
167. ———— and D. L. FOWLER. 1951. *A Fusarium* wilt of radish in Wisconsin. *Ibid.* **41:** 30.
168. ———— and J. C. WALKER. 1951. Mosaic resistance in cabbage. *Ibid.* **41:** 1083–1090.
169. PRYOR, D. E., and R. E. WESTER. 1946. Relative resistance and susceptibility of U.S. 243 and U.S. 343 lima beans to lima-bean mosaic. *Ibid.* **36:** 170–172.
170. ———— and T. W. WHITAKER. 1942. The reaction of cantaloupe strains to powdery mildew. *Ibid.* **32:** 995–1004.
171. RAMSEY, G. B., B. C. HEIBERG and J. S. WIANT. 1946. *Diplodia* rot of onions. *Ibid.* **36:** 245–251.
172. REDDICK, D., and L. C. PETERSON. 1945. Empire—a blight resistant variety. Am. Potato Jour. **22:** 357–362.
173. ———— and ————. 1947. New blight-resistant varieties. *Ibid.* **24:** 319–336.
174. ———— and ————. 1950. Additional blight-resistant varieties. *Ibid.* **27:** 1–10.
175. REYNARD, J. B., and C. F. ANDRUS. 1945. Inheritance of resistance to the collar-rot phase of *Alternaria solani* on tomato. Phytopath. **35:** 25–36.
176. RICHARDS, B. L., and W. H. BURKHOLDER. 1943. A new mosaic disease of beans. *Ibid.* **33:** 1215–1216.
177. RIEDL, W. A., F. J. STEVENSON and R. BONDE. 1946. The Teton potato: a new variety resistant to ring rot. Am. Potato Jour. **23:** 379–389.
178. RIEMAN, G. H. 1931. Genetic factors for pigmentation in the onion and their relation to disease resistance. Jour. Agr. Res. **42:** 251–278.
179. ———— and J. S. MCFARLANE. 1943. The resistance of the Sebago variety to yellow dwarf. Am. Potato Jour. **20:** 277–283.
180. RIOLLANO, H. 1943. Louisiana Red Creole a new promising variety for Puerto Rico. Proc. Am. Soc. Hort. Sci. **43:** 272–274.
181. ————, J. ADSUAR and A. RODRÍGUEZ. 1948. Breeding peppers resistant to a Puerto Rican type of mosaic. *Ibid.* **51:** 415–416.
182. ROQUE, A. 1936–38. Ann. Rep., Agr. Exp. Sta. Rio Piedras, Puerto Rico **1935–36:** 47–48; **1937–38:** 44–45.

183. Ross, H. 1952. Studies on mosaic resistance in the potato. Proc. Conf. Potato Virus Dis., Wageningen-Lisse 1951: 60–67.
184. ———— and M.-L. Baerecke. 1950. Selection for resistance to mosaic virus (diseases) in wild species and in hybrids of wild species of potatoes. Am. Potato Jour. **27**: 275–284.
185. Rozendaal, A. 1952. Demonstrations of experiments with potato viruses. Proc. Conf. Potato Virus Dis., Wageningen-Lisse 1951: 63–65.
186. Rudorf, W., and P. Schaper. 1951. Grundlagen und Ergebnisse der Züchtung Krautfäuleresistenter Kartoffelsorten. Zeits. Pflanzenzücht. **30**: 29–88.
187. Schaal, L. A., W. C. Edmundson and R. Kunkel. 1949. Yampa, a new scab-resistant potato. Am. Potato Jour. **26**: 335–342.
188. Schaible, L., O. S. Cannon and V. Waddoups. 1951. Inheritance of resistance to *Verticillium* wilt in a tomato cross. Phytopath. **41**: 986–990.
189. Scheffer, R. P., and J. C. Walker. 1952. Distribution of *Fusarium* resistance in the tomato plant. *Ibid.* **42**: 474.
190. Schlumberger, O. 1943. Die Zuverlässigkeit der Kartoffelkrebs-Prüfungen. Forschungsdienst. **16**: 215–220.
191. Schroeder, W. T. 1951. Field reaction of seventeen tomato varieties to three diseases in 1949 and 1950 at Geneva, New York. Plant Dis. Rep. **35**: 160–161.
192. ———— and J. C. Walker. 1942. Influence of controlled environment and nutrition on the resistance of garden pea to *Fusarium* wilt. Jour. Agr. Res. **65**: 221–248.
193. Schultz, E. S., F. J. Stevenson and R. V. Akeley. 1947. Resistance of potato to virus Y, the cause of veinbanding mosaic. Am. Potato Jour. **24**: 413–419.
194. Schultz, H. K., and L. L. Dean. 1947. Inheritance of curly top disease reaction in the bean, *Phaseolus vulgaris*. Jour. Am. Soc. Agron. **39**: 47–51.
195. Shapovalov, M., and B. A. Rudolph. 1939. Essar, a new *Verticillium* wilt resistant canning tomato. Seed World **46**(13): 12–13.
196. ———— and J. W. Lesley. 1940. Wilt resistance of the Riverside variety tomato to both *Fusarium* and *Verticillium* wilts. Phytopath. **30**: 760–768.
197. Shifriss, O., C. H. Myers and C. Chupp. 1942. Resistance to mosaic virus in the cucumber. *Ibid.* **32**: 773–784.
198. Smith, P. G. 1948. Powdery mildew resistance in cucumber. *Ibid.* **38**: 1027–1028.
199. ————. 1950. Downy mildew immunity in spinach. *Ibid.* **40**: 65–68.
200. ———— and M. W. Gardner. 1951. Resistance in tomato to the spotted-wilt virus. *Ibid.* **41**: 257–260.
201. ———— and P. A. Minges. 1951. Resistance of strains of California Wonder pepper to *Phytophthora* root rot. Plant Dis. Rep. **35**: 509.
202. Snyder, W. C., K. F. Baker and H. N. Hansen. 1946. Interpretation of resistance to *Fusarium* wilt in tomato. Science **103**: 707–708.
203. Steinbauer, C. E. 1948. A sweetpotato from Tinian Island highly resistant to *Fusarium* wilt. Proc. Am. Soc. Hort. Sci. **52**: 304–306.
204. Stelzner, G. 1950. Virusresistenz der Wildkartoffeln. Zeits. Pflanzenzücht. **29**: 135–158.
205. Stevenson, F. J., and J. R. Livermore. 1949. The Saranac potato: a new variety promising in Australia. Am. Potato Jour. **26**: 45–46.
206. ————, L. A. Schaal, C. F. Clark and R. V. Akeley. 1942. Potato-scab gardens in the United States. Phytopath. **32**: 965–971.

207. ————, E. S. SCHULTZ, R. V. AKELEY and L. C. CASH. 1952. Late blight immunity in the potato. *Ibid.* **42**: 277–280.
208. STOLL, K. 1950. Resistenzprüfungen an Leguminosen gegenüber dem Fusskrankheitserreger *Ascochyta pinodella* Jones. Zeits. Pflanzenzücht. **29**: 175–192.
209. TEDIN, O. 1950. Svalöfs Evapotatis (42096). Ny, Kraftimmum, mycket tidig sort. Sveriges Utsädesför. Tidskr. **60**: 215–219.
210. THOMAS, H. R., H. JORGENSEN and R. E. WESTER. 1952. Resistance to downy mildew in lima bean, and its inheritance. Phytopath. **42**: 43–45.
211. ———— and W. J. ZAUMEYER. 1950. Inheritance of symptom expression of pod mottle virus. *Ibid.* **40**: 1007–1010.
212. ————, W. J. ZAUMEYER and H. JØRGENSEN. 1951. Inheritance of resistance to lima-bean mosaic virus in the lima bean. *Ibid.* **41**: 231–234.
213. THOMPSON, R. C. 1944. Reaction of *Lactuca* species to the aster yellows virus under field conditions. Jour. Agr. Res. **69**: 119–125.
214. THUNG, T. H. 1947. Potato diseases and hybridization. Phytopath. **37**: 373–381.
214*a*. ————. 1949. Zwartrot van kool. Tijdschr. over Plantenziek. **55**: 191–195.
215. TIMS, E. C. 1946. Some shallot diseases in Louisiana. Plant Dis. Rep. **30**: 335–338.
216. TOWNSEND, G. R., R. A. EMERSON and A. G. NEWHALL. 1946. Resistance to *Cercospora apii* Fres. in celery (*Apium graveolens* var. *dulce*). Phytopath. **36**: 980–982.
217. ———— and B. L. WADE. 1943. Close-up of something new in snap beans. Two varieties developed for Florida etc. Southern Seedsman **6**(3) : 9, 40.
218. VAN HALTERN, F. 1943. No more bad years for watermelons. New wilt-resistant variety developed at Georgia A.E.S. *Ibid.* **6**(1) : 1.
219. ————. 1951. Georgia 47 cantaloupe, mildew resistant. *Ibid.* **14**(11) : 31, 45.
220. VAUGHN, J. R. Factors affecting the nature of resistance of potatoes to scab. Phytopath. **38**: 27–28.
221. WADE, B. L., and C. F. ANDRUS. 1941. A genetic study of common bean mosaic under conditions of natural field transmission. Jour. Agr. Res. **63**: 389–393.
222. WALKER, J. C. 1948. Diseases of cabbage and related plants. U. S. Dept. Agr., Farm. Bul. 1439.
223. ————. 1950. Environment and host resistance in relation to cucumber scab. Phytopath. **40**: 1094–1102.
224. ———— and R. E. FOSTER. 1946. Plant nutrition in relation to disease development. III. *Fusarium* wilt of tomato. Am. Jour. Bot. **33**: 259–264.
225. ———— and J. P. JOLIVETTE. 1948. Yellows-resistant varieties of cabbage in the early and mid-season roundhead group. U. S. Dept. Agr., Cir. 775.
226. ————, H. A. JONES, and A. E. CLARKE. 1944. Smut resistance in an *Allium* species hybrid. Jour. Agr. Res. **69**: 1–8.
227. ———— and R. H. LARSON. 1948. Development of clubroot resistance in cabbage. Phytopath. **38**: 28.
228. ———— and ————. 1951. Progress in the development of clubroot-resistant cabbage. *Ibid.* **41**: 37.
229. ————, ————, R. E. FOSTER and J. E. KUNTZ. 1948. Yellows-resistant cabbage varieties in the Danish Ballhead-Hollander group. U. S. Dept. Agr., Cir. 776.

230. ————, C. F. Pierson and A. B. Wiles. 1953. Two new scab-resistant cucumber varieties. Phytopath. **53:** 215–217.
231. ———— and G. S. Pound. 1947. Improvement of cabbage for disease resistance. *Ibid.* **37:** 23.
232. ———— and A. B. Wiles. 1951. Development of a scab-resistant cucumber for Wisconsin. *Ibid.* **41:** 37.
233. Walker, M. N. 1945. The Blacklee watermelon. Seed World **57**(10) : 12, 14.
234. Walter, J. M., and R. A. Conover. 1952. Hereditary resistance to late blight of tomato. Phytopath. **42:** 197–199.
235. Warid, W. A., and E. C. Tims. 1952. Studies on the inheritance of resistance to downy mildew in onion incited by *Peronospora destructor*. *Ibid.* **42:** 22.
236. Wark, D. C. 1950. The inheritance of resistance to *Ascochyta pisi* Lib. in *Pisum sativum* L. Austral. Jour. Agr. Res. **1:** 382–390.
237. Watson, R. D. 1945. Sweet potato soil rot slip treatment and varietal reaction tests in Texas. Plant Dis. Rep. **29:** 240–241.
238. Webb, R. E., R. H. Larson and J. C. Walker. 1951. Naturally occurring strains of the potato leaf roll virus. Am. Potato Jour. **28:** 667–671.
238*a*. ————, ———— and ————. 1952. Relationships of potato leaf roll virus strains. Wis. Agr. Exp. Sta., Res. Bul. 178.
239. Weimer, J. L. 1940. Methods of value in breeding Austrian Winter field peas for disease resistance in the south. Phytopath. **30:** 155–160.
240. ————. 1947. Resistance of *Lathyrus* spp. and *Pisum* spp. to *Ascochyta pinodella* and *Mycosphaerella pinodes*. Jour. Agr. Res. **75:** 181–190.
241. Welch, A., and I. E. Melhus. 1942. Wilt resistance in F_1 hybrid watermelons. Phytopath. **32:** 181–182.
242. Wellhausen, E. J., L. M. Roberts, J. M. Munox and C. Linton. 1949. Frijol Rocamex 1, 2, y 3, tres variedades majoradas para siembras de temporal en la mesa central. Foll. Divulg. Secret. Agr. Mexico 8.
243. Wellman, F. L. 1943. Increase of pathogenicity in tomato-wilt *Fusarium*. Phytopath. **33:** 175–193.
244. ————. 1943. Comparative toxic effect of extracts from mild and virulent isolates of tomato-wilt *Fusarium*. *Ibid.* **33:** 1004–1017.
245. ———— and D. J. Blaisdell. 1941. Pathogenic and cultural variation among single-spore isolates from strains of the tomato-wilt *Fusarium*. *Ibid.* **31:** 103–120.
246. Wells, D. G., W. W. Hare and J. C. Walker. 1949. Evaluation of resistance and susceptibility in garden pea to near-wilt in the greenhouse. *Ibid.* **39:** 771–779.
247. ————, J. C. Walker and W. W. Hare. 1949. A study of linkage between factors for resistance to wilt and near-wilt in garden peas. *Ibid.* **39:** 907–912.
248. Wheeler, E. J., F. J. Stevenson and H. C. Moore. 1944. The Menominee potato: a new variety resistant to common scab and late blight. Am. Potato Jour. **21:** 305–311.
249. Whitaker, T. W., and G. N. Davis. 1946. Cantaloupes 6 and 7. Southern Seedsman, February.
250. ———— and D. E. Pryor. 1941. The inheritance of resistance to powdery mildew (*Erysiphe cichoracearum*) in lettuce. Phytopath. **31:** 534–540.
251. ———— and ————. 1942. Genes for resistance to powdery mildew in *Cucumis melo*. Proc. Am. Soc. Hort. Sci. **41:** 270–272.

252. ———— and ————. 1945. The reaction of 21 species in the Cucurbitaceae to artificial infection with cantaloupe powdery mildew (*Erysiphe cichoracearum* DC.) Phytopath. **35**: 533–534.
253. ———— and ————. 1947. Correlated resistance of leaves, cotyledons, and stems of *Cucumis melo* L. to cantaloupe powdery mildew (*Erysiphe cichoracearum* DC.). *Ibid.* **37**: 865–867.
254. WILSON, J. D. 1940. Relative susceptibility of celery varieties to *Fusarium* yellows in Ohio. Ohio Agr. Exp. Sta., Bimo. Bul. **25**: 7–15.
255. ————. 1947. Anthracnose and its effect on tomato varieties. Food Packer **28**: 66–67.
256. ————. 1951. Ohio MR 17. A new mosaic tolerant pickling cucumber. Ohio Agr. Exp. Sta., Res. Cir. 10.
257. ———— and H. A. RUNNELS. 1949. Tomato anthracnose. Comparative susceptibility of varieties and their response to spraying. Ohio Agr. Exp. Sta., Res. Bul. 685.
258. ———— and J. J. WILSON. 1944. A mosaic-tolerant, pickling-type cucumber. Ohio Agr. Exp. Sta., Bimo. Bul. **29**: 110–113.
259. WOLLENWEBER, H. W. 1927. Die Wirtelpilz-Welkekrankheit (Verticilliose) der Kartoffel. Biol. Reichsanst. Land und Forstw. Flugbl. 84.
260. YU, T. F. 1937. On the occurrence of *Colletotrichum lindemuthianum* (Sacc. & Magn.) on broad bean seeds. Chinese Bot. Soc. Bul. **3**: 1–24.
261. ZAUMEYER, W. J. 1942. Reaction of pea varieties to *Septoria pisi*. Phytopath. **32**: 64–70.
262. ————. 1947. Control of bean diseases. U. S. Dept. Agr., Yearbook **1943–1947**: 333–337.
263. ———— and L. L. HARTER. 1941. Inheritance of resistance to six physiologic races of bean rust. Jour. Agr. Res. **63**: 599–622.
264. ———— and ————. 1943. Inheritance of symptom expression of bean mosaic virus 4. *Ibid.* **67**: 295–300.
265. ———— and ————. 1946. Pintos 5 and 14. New rust-resistant beans for dryland areas of the west. Southern Seedsman **9**(8) : 15, 50, 54.
266. ZAUMEYER, W. J., and H. R. THOMAS. 1949. Bean diseases and their control. U. S. Dept. Agr., Farm. Bul. 1692.

Future Contents of

THE BOTANICAL REVIEW

Articles Received and Awaiting Publication

Wood Fiber Length as Related to Position in Tree and Growth	STEPHEN H. SPURR *University of Minnesota*
Compression Wood in Conifers as a Morphogenetic Phenomenon	
Seed Germination Problems in the Umbelliferae	RICHARD ROBINSON *University of California*
Suggestions for the Classification and Nomenclature of Fossil Spores and Pollen Grains	DIVYA DARSHAN PANT *University of Allahabad*
Heart Rots in Living Trees	W. W. WAGENER and R. W. DAVIDSON *U. S. Dept. of Agriculture*
The Cryptogamic Flora of the Arctic:	
Algae	WILLIAM RANDOLPH TAYLOR *University of Michigan*
Algae: Planktonic groups	R. ROSS *British Museum, London*
Bacteria	C. D. KELLY *McGill University*
Bryophytes	WILLIAM CAMPBELL STEERE *Stanford University*
Fungi	ROLF SINGER *Farlow Herbarium, Cambridge*
Lichens	EILIF DAHL *Yale University*
On Modified Hyphae of Hymenomycetes	PAUL L. LENTZ *U. S. Bureau of Plant Industry*
Cytogenetics of the Vegetable Crops. I. Monocotyledons	S. H. YARNELL *U. S. Department of Agriculture*
The Morphology of Leaves	VERA L. RYDER *Oregon State College*
In Vitro Culture of Plant Embryos and Factors Controlling Their Growth	JAQUES RAPPAPORT *University of Virginia*
Ecological Processes and Vegetation of the Maritime Strand in the Southeastern United States	HENRY J. OOSTING *Duke University*
Some Historical Chapters on Tree Growth	R. A. STUDHALTER *Texas Technological College*
The Shoot Apex in Angiosperms	EARNEST M. GIFFORD *University of California*
Growth Rings and Climate	WALDO S. GLOCK *Macalester College*

4184